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Linking biodiversity, landscape dynamics and agricultural policies to inform conservation on farmland:

The case of Mediterranean farmland birds

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In memory of my Grandfather
(1919-2012)

To my Grandmother and Mother
To Luís
To Miguel

Em memória do meu Avô
(1919-2012)

Para a minha Avó e a minha Mãe
Para o Luís
Para o Miguel

Preliminary remark

In the elaboration of this dissertation, and in compliance with number 2 of Article 4 of the General Regulation of the Third Cycles of Studies of the University of Porto and Article 31 of D.L. 74/2006, of March 24, with the new wording introduced by D.L. 63/2016, of 13 September, it was made the full use of a coherent set of research articles already published in peer-reviewed journals with selection committees of recognized international merit, which are part of some of the chapters of this thesis. Taking into account that these works were carried out with the collaboration of other authors, the candidate elucidates that in all of them she participated actively in its conception, in obtaining, analyzing and discussing the results, as well as in the preparation of its published form.

List of articles

Chapter 2 - Santana, J., Reino, L., Stoate, C., Borralho, R., Schindler, S., Moreira, F., Bugalho, M., Ribeiro, P.F., Santos, J.L., Vaz, A., Morgado, R., Miguel, P. & Beja, P. (2014). Mixed effects of long-term conservation investment in Natura 2000 farmland. *Conservation Letters*, **7**(5), 467-477. doi:10.1111/conl.12077 (Impact Factor [2015] = 7.128)

Chapter 3 - Santana, J., Reino, L., Stoate, C., Moreira, F., Ribeiro, P.F., Santos, J.L., Rotenberry, J. T. & Beja, P. (2017). Combined effects of landscape composition and heterogeneity on farmland avian diversity. *Ecology and Evolution*, **7**(4), 1212-1223. doi:10.1002/ece3.2693 (Impact Factor [2015] = 2.537)

Chapter 4 - Santana, J., Miguel, P., Reino, L., Moreira, F., Ribeiro, P.F., Santos, J.L., Rotenberry, J. T. & Beja, P. (2017). Using beta diversity to inform agricultural policies and conservation actions on Mediterranean farmland. *Journal of Applied Ecology*. doi:10.1111/1365-2664.12898 (Impact Factor [2015] = 5.196)

Nota prévia

Na elaboração desta dissertação, e nos termos do número 2 do Artigo 4º do Regulamento Geral dos Terceiros Ciclos de Estudos da Universidade do Porto e do Artigo 31º do D.L. 74/2006, de 24 de Março, com a nova redação introduzida pelo D.L. 63/2016, de 13 de Setembro, foi efectuado o aproveitamento total de um conjunto coerente de trabalhos de investigação objecto de publicação em revistas com comissões de selecção de reconhecido mérito internacional, os quais integram alguns dos capítulos da presente tese. Tendo em conta que os referidos trabalhos foram realizados com a colaboração de outros autores, a candidata esclarece que, em todos eles, participou ativamente na sua concepção, na obtenção, análise e discussão de resultados, bem como na elaboração da sua forma publicada.

Lista de artigos

Capítulo 2 - Santana, J., Reino, L., Stoate, C., Borralho, R., Schindler, S., Moreira, F., Bugalho, M., Ribeiro, P.F., Santos, J.L., Vaz, A., Morgado, R., Miguel, P. & Beja, P. (2014). Mixed effects of long-term conservation investment in Natura 2000 farmland. *Conservation Letters*, **7**(5), 467-477. doi:10.1111/conl.12077 (Impact Factor [2015] = 7.128)

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The PhD is a very long journey. So long that one may believe it won't ever end. Fortunately, this one seems to have finally reaching its end. Just like in a race, we start the PhD full of energy, enthusiasm and motivation. However, at some point we become so tired that we doubt if we can really finish it. From time to time we remember why we started it, and then gain a little more strength to continue. Finally, when there are only a few kilometers to go, we only feel the pain and the need to finish what we have started, with the hope that at the end we can look back and see that what we have achieved was far greater than what we have lost. Fortunately, I resisted to reach this stage and I am able to see that this is real and to write these words!

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Abstract

About half the world's terrestrial surface is managed for agriculture, and an important proportion of global biodiversity is found on farmland. Therefore, conserving biodiversity on farmland is an essential element of worldwide efforts for reversing global biodiversity decline. However, this goal has been hindering by the pervasive intensification of farming practices, which have contributed to an increase in the rate of biodiversity losses during the last decades. Furthermore, managing farmland landscapes to enhance biodiversity is complex, as biological diversity is constrained by a number of interacting and changing socioecological factors including agricultural policies, socio-economic drivers and biophysical conditions, which may affect the effectiveness of conservation actions.

This thesis addresses these issues using three case studies focusing on breeding bird assemblages living in Mediterranean farmland landscapes of southern Portugal. This model system was used to understand how biological diversity may vary in space and time in relation to landscape dynamics, agricultural policies and conservation actions, which is a knowledge required to inform conservation actions on farmland. The studies focused on (i) how to enhance the effectiveness of conservation investment in farmland protected areas; (ii) how to manage farmland landscapes for biodiversity conservation within and outside protected areas; and (iii) how to link biodiversity measures to landscape features to inform conservation actions and agricultural policies.

These studies provided insights to the design and evaluation of conservation actions by showing that enhancing the effectiveness of conservation investment in farmland protected areas may require a greater focus on the wider biodiversity in addition to that currently devoted to flagship species, as well as improved matching between conservation and agricultural policies. Also, it was shown that managing farmland landscapes for conservation needs to consider both composition and heterogeneity, and that maximising the prevalence of biodiversity-friendly crops may be particularly important in landscapes where a range of species of conservation concern is strongly associated with the production component of the landscape. Finally, it was shown that the analyses of spatial variation in species composition (beta diversity) is required to understand the impacts of agricultural policies and conservation actions on farmland biodiversity, as it provides information on how changes in landscape heterogeneity affects local (alpha diversity) and regional (gamma diversity) species richness and composition. However, it also highlighted the need to evaluate beta diversity changes against specific conservation goals.

Overall, this thesis provides novel information on the drivers of biodiversity change in agricultural landscapes, showing in particular the cascading effects that may

occur from agricultural policies through landscape dynamics to alpha, beta and gamma diversity patterns, which in turn may be used to improve biodiversity conservation and management on farmland.

Keywords: agriculture intensification, agriculture policies, biodiversity conservation, biodiversity loss, conservation actions, diversity metrics, landscape composition, landscape heterogeneity, land-use changes, Mediterranean farmland, protected areas.

Resumo

Cerca de metade da superfície terrestre do mundo é utilizada para a agricultura, e uma proporção importante da biodiversidade global encontra-se em áreas agrícolas. Assim, a conservação da biodiversidade em áreas agrícolas é uma componente essencial dos esforços mundiais para reverter o declínio global da biodiversidade. No entanto, esse objetivo tem vindo a ser dificultado pela intensificação generalizada das práticas agrícolas, que tem contribuído para aumentar a taxa de declínio da biodiversidade nas últimas décadas. Além disso, a gestão de paisagens agrícolas para beneficiar a biodiversidade é complexa, uma vez que a diversidade biológica é condicionada pelas interacções e permanente modificação de um conjunto de fatores socioecológicos, incluindo políticas agrícolas, processos socioeconómicos e condições biofísicas da paisagem, que podem afetar a eficácia das ações de conservação.

Esta tese aborda estas questões utilizando três casos de estudo centrados nas comunidades de aves de áreas agrícolas Mediterrânicas do sul de Portugal. Este sistema foi utilizado para entender como a diversidade biológica pode variar no espaço e no tempo em relação à dinâmica da paisagem, políticas agrícolas e ações de conservação, conhecimento este que é indispensável para informar as ações de conservação em áreas agrícolas. Os estudos focaram em (i) como aumentar a eficácia do investimento em conservação em áreas protegidas de terras agrícolas; (ii) como gerir paisagens agrícolas para a conservação da biodiversidade dentro e fora das áreas protegidas; e (iii) como ligar as medidas de biodiversidade às características da paisagem para informar as ações de conservação e as políticas agrícolas. Estes estudos produziram conhecimentos essenciais para a delineamento e avaliação de ações de conservação, mostrando que o aumento da eficácia do investimento em áreas protegidas pode exigir um enfoque mais alargado na biodiversidade a par do esforço atualmente já dedicado a espécies emblemáticas, bem como uma melhor articulação entre conservação e políticas agrícolas. Além disso, foi demonstrado que a gestão de paisagens agrícolas para a conservação deve considerar tanto a composição como a heterogeneidade, sendo que em paisagens agrícolas onde diversas espécies com estatuto de conservação desfavorável estão fortemente associadas com a componente de produção, i.e. com os habitats agrícolas, deve maximizar-se a prevalência de culturas favoráveis à biodiversidade. Finalmente, foi demonstrado que a análise da variação espacial da composição de espécies (diversidade beta) é necessária para compreender os impactos das políticas agrícolas e ações de conservação na biodiversidade de áreas agrícolas, pois fornece informações sobre como as mudanças na heterogeneidade da paisagem afetam a riqueza e a composição das espécies a nível local (diversidade alfa)

e regional (diversidade gama). No entanto, também foi destacada a necessidade de avaliar as mudanças de diversidade beta em relação aos objetivos específicos de conservação.

Em termos gerais, esta tese fornece novas informações sobre os fatores que influenciam as alterações da biodiversidade em áreas agrícolas, mostrando, em particular, a cascata de efeitos que podem ocorrer desde as políticas agrícolas até aos padrões de diversidade alfa, beta e gama, mediados pelas dinâmicas da paisagem, e as implicações destes processos para melhorar a conservação e gestão da biodiversidade.

Palavras-chave: intensificação agrícola, políticas agrícolas, conservação da biodiversidade, perda de biodiversidade, ações de conservação, métricas de diversidade, composição da paisagem, heterogeneidade da paisagem, mudanças no uso do solo, áreas agrícolas mediterrânicas, áreas protegidas.

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Abbreviations

AES	Agri-environment scheme
AIC	Akaike information criterion
AICc	Akaike information criterion corrected for small sample sizes
BACI	Before-After-Control-Impact
CAP	Common Agriculture Policy
CI	95% confidence interval
EU	European Union
GLMMs	Generalized linear mixed models
LIFE	LIFE-Nature programme
N2000	Natura 2000 network
PA	Protection area
PC	Principal component
$PC\#_{high}$	Principal component of habitat variables in high-intensity farmland
$PC\#_{low}$	Principal component of habitat variables in low-intensity farmland
PCA	Principal component analysis
pCCA	Partial constrained correspondence analysis
SPA	Special Protection Area, Directive 79/409/EEC
SPEC1-3	Species with unfavorable conservation status in Europe
w_i	Akaike weight
w_i+	Sum of Akaike weights
α-diversity	Alpha diversity
β-diversity	Beta diversity
β_{Repl}	Species replacement component of beta diversity
$\beta_{RichDiff}$	Species richness difference component of beta diversity
β_{tot}	Total beta diversity
γ-diversity	Gamma diversity

Chapter 1

General introduction

“Only within the 20th Century has biological thought been focused on ecology, or the relation of the living creature to its environment. Awareness of ecological relationships is - or should be - the basis of modern conservation programs, for it is useless to attempt to preserve a living species unless the kind of land or water it requires is also preserved. So delicately interwoven are the relationships that when we disturb one thread of the community fabric we alter it all - perhaps almost imperceptibly, perhaps so drastically that destruction follows."

Essay on the Biological Sciences, In: Good Reading
Rachel Carson (1956)

1. General introduction

1.1 Biodiversity conservation

Biodiversity (i.e. the contraction of ‘biological diversity’ or ‘biotic diversity’) is a synonym for the ‘variety of life’, which may include genetic, taxonomic/species and ecological diversity, and the processes where these hierarchical levels are included, i.e. composition (the identity and variety of elements), structure (the physical organization and pattern of elements), and function (ecological and evolutionary processes) (Noss 1990). However, the term ‘biodiversity' also expresses the importance of that variety, of the crisis represented by its loss, and of the need for conservation action. In fact, biodiversity is a social-political construction reflecting concerns over the loss of the natural environment, and thus its contents appear intrinsically connected to conservation biology. Since its first usage in 1986, to entitle the ‘National Forum on BioDiversity’, biodiversity became a term widely used and recognized across a range of arenas, including by biologists, ecologist, conservationists, politicians and the general public. Its importance was officially recognized in 1992 by more than 50 nations signatory to “The Convention on Biological Diversity", which increased to 150 signatures by 2016 (The Convention on Biological Diversity 2016), wherein biological diversity [biodiversity] was recognised as being “the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species, and of ecosystems.” This thesis focused on the composition and structure of taxonomic/species diversity, because this is a large part of the focus of biodiversity conservation at local, landscape and regional scales.

Biodiversity is declining worldwide. Many studies indicate that we are entering the sixth mass extinction, reporting loss of genetic diversity, species extinctions, reduction of species richness, species abundance and population ranges decreases for all taxa, and changes and destruction of habitats, landscapes and even entire ecosystems (Raven 1987; Myers 1990; Dirzo & Raven 2003; Wake 2008; Barnosky *et al.* 2011, Ehrlich &. Ehrlich 2013; Ceballos *et al*. 2010, 2015). Recent conservative estimates indicate that extinction rates have abruptly increased since 1900s, corresponding to the rise of industrial society. The average rate of vertebrate species extinctions over the last century is up to 100 times higher than the usual rate observed in-between the five previous mass extinctions (Ceballos *et al*. 2015). Based on the 2014 IUCN red list, 477 vertebrates became “extinct”, “extinct in the wild” or “possible extinct” since 1900 (69

mammals, 80 birds, 24 reptiles, 146 amphibians and 158 fishes), numbers that would have taken, depending on the taxa, between 800 and 10,000 years to disappear without human activities (Ceballos *et al*. 2015). This is even more disturbing if we consider that the 1.2 millions of species taxonomically described correspond to about 15% of the existing species (Mora *et al.* 2011), which means that many species will certainly became extinct without even being discovered. This catastrophic scenario of biodiversity loss has drawn worldwide attention, driving energies to conserve biodiversity, and many efforts have been made in the last decades to identify sources of pressure to respond to reducing biodiversity losses (Butchart *et al.* 2010). However, despite some local successes and increasing responses to address this problem, continued declines have occurred since the 1970s, along with increasing pressures on biodiversity (Butchart *et al.* 2010). Efforts to conserve biodiversity thus need to be greatly intensified, together with efforts to reduce pressures to avoid irreversible losses (Butchart *et al.* 2006; Hoffmann *et al.* 2010).

Conserving biodiversity is important because its loss represents a major threat to ecosystem service and human wellbeing (Dirzo & Raven 2003; Wake 2008; Barnosky *et al.* 2011; Ehrlich &. Ehrlich 2013; Ceballos *et al*. 2010, 2015, Fig. 1.1). Benefits for human needs may be directly supplied by ecosystem services represented by “the conditions and processes of ecosystems that generate, or help generate, benefits for people”, that result “from the interactions among plants, animals, and microbes in the ecosystem, as well as biotic, abiotic, and human-engineered components of social-ecological systems” (Guerry *et al.* 2015), but also by sustaining final services, e.g., the generation of habitats that support a direct resource (Fisher *et al.* 2009). However conservation based on ecosystem services and human needs may fail when the focus of conservation actions is ‘useless’ for human needs or for ‘ecosystem functioning’. Ghilarov (2000) argued that biodiversity should be valued by its intrinsic value such as the uniqueness of species, the right of species to exist, and the irreversible nature of extinction (Hamilton *et al.* 2005, Fig. 1.1). However, in a market-based world, it would be very difficult to convince governments, policy makers and people in general to invest in biodiversity conservation based only in the intrinsic value of biodiversity. Therefore, the global commitment to protect biodiversity for 2020 recognizes the intrinsic value of biological diversity together with its importance for human needs and for ecosystem function, as a need to “act as practical tool for translating the principles of Agenda 21 into reality” (The Convention on Biological Diversity 2016).

Human activities have been identified as the main factor responsible for the ongoing biodiversity decline (Ceballos *et al*. 2015), primarily by destroying pristine habitats, with uninterrupted forest clearing and burning for agriculture, forestry and

urbanization; or secondarily by changing practices which influence land uses by intensifying activities that disrupt an existing equilibrium from the established activities, or even by other activities such as hunting, persecution, introduction of exotic species, and global warming (Bignal & McCrachken 2000; Fuller & Ausden 2008; Hinsley & Gillings 2012). Most of the places on earth have in one way or another suffered some human intervention in the past. However, since the industrialization of farming (i.e. intensification) after the second world war (1939-1945), the rate and extent of landscape change, and its impacts on biodiversity, may be at least as great as at any time in the past (Bignal & McCrachken 2000; Fuller & Ausden 2008; Barnosky *et al.* 2011; Hinsley & Gillings 2012). Intensification includes increasing levels of mechanisation and chemical use, simplification of farming practices, increases in farm size, changes in crop types, changes in the times of sowing and harvesting, the spread of monocultures, increased stocking densities, modification of soil characteristics, and the reduction of non-farmed habitats (Stoate *et al*. 2001; Vickery *et al*. 2001; Robinson & Sutherland 2002; Newton 2004; Donald *et al.* 2006). Also, many low-intensity farming systems have been replaced by commercial forestry, and urban and industrial areas have expanded (Bignal & McCrachken 2000).

The context

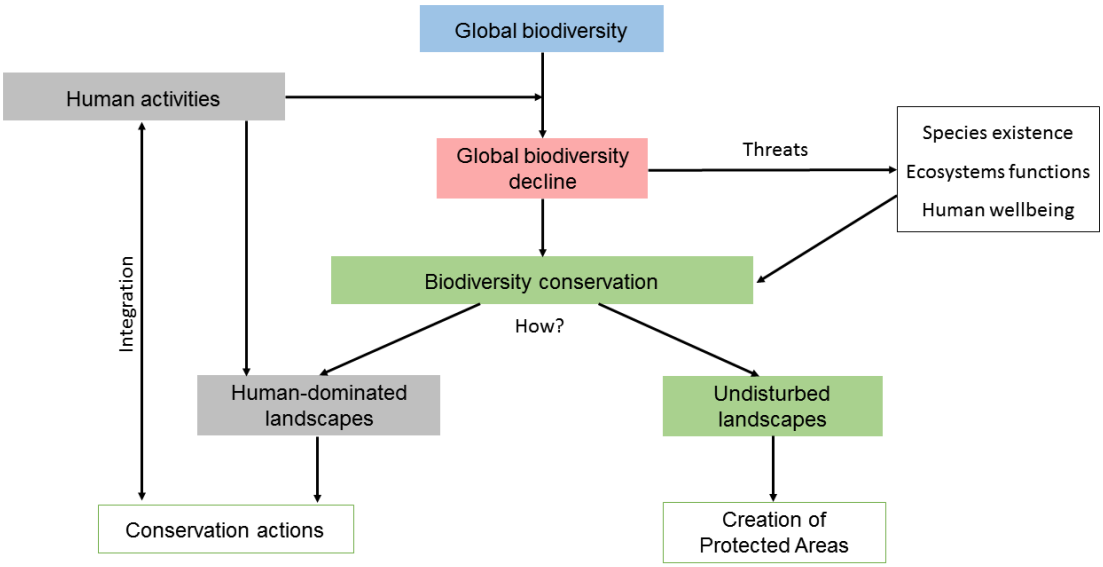

Fig.1.1 – The biodiversity conservation context. The need to conserve biodiversity flows from biodiversity declines due to human activities that threaten species existence, ecosystem functions and human wellbeing. Biodiversity conservation must be focused both on protecting more natural undisturbed landscapes, and by performing conservation actions within human-dominated landscapes, where integration with local human activities is required.

Strategies to reverse global biodiversity decline may involve the establishment of protected areas to safeguard remaining pristine or mainly natural habitats from future disturbance (Margules & Pressey 2000, Fig.1.1). However, protected areas will not be enough to protect global biodiversity as they are insufficient to ensure the maintenance of ecological and evolutionary processes, which typically take place over scales far larger than the size of even the biggest protected areas (Soulé & Sanjayan 1998; Hames et al. 2001), and an important fraction of global biodiversity remains on human-dominated landscapes (Pimentel *et al.* 1992; Franklin 1993; Bignal & McCracken 1996; Pain & Pienkowski 1997; Krebs *et al.* 1999; Hames *et al*. 2001; Tscharntke *et al.* 2005). Hence, maintaining biodiversity within the human-dominated landscapes is essential for conservation of biodiversity where conservation actions need to be integrated with economic activities; funding is required to implement conservation rules and regulations, as well as incentives, subsidies, and other measures designed to encourage sustainable use of biodiversity (Hames *et al.* 2001).

1.2 Biodiversity conservation on farmland

About half of the world's terrestrial surface is managed for agriculture (FAO 2011), making farmland the most important human-dominated landscape where an important proportion of global biodiversity may be found (Hames *et al.* 2001, Krebs *et al.* 1999). Conserving biodiversity in farmland landscapes is thus a current major goal to reversing biodiversity decline worldwide (Krebs *et al.* 1999; Donald *et al.* 2006; Sutcliffe *et al.* 2015). In Europe, land cover is mostly the result of millennia of human management in alternation with abandonment periods, which have molded the landscapes and thus the composition and structure of its biological assemblages through time (Blondel & Aronson 1999; Bignal & McCrachken 2000). Certain types of these ancient landscape structures are maintained by low-intensity farming practices, maintaing a complex matrix of productive fields interspersed with natural or semi-natural habitats, which supports an important portion of European biodiversity (Kleijn *et al.* 2009; Bugalho *et al.* 2011; Doxa *et al.* 2012), including many species of conservation concern (BirdLife International 2004; Kleijn *et al.* 2011). In most of these areas, farm structures and farming practices are closely adapted to local conditions, including livestock systems associated with natural or semi-natural pastures, low-intensity arable systems in rotation with fallows, low-intensity permanent crops (e.g. traditional orchards and olive groves), and mixed farming systems with arable/or permanent crops with livestock, which provide a mosaic of low intensity agriculture and valuable landscape features supporting high species biodiversity (Oppermann *et al.* 2012). However, agricultural policies over the last

decades promoting intensification of agricultural practices have been conducive to landscape simplification at all spatial scales, thus contributing to strong declines in farmland biodiversity (Krebs *et al*. 1999; Donald *et al.* 2001; Tilman *et al*. 2001; Stoate *et al.* 2001.

Conserving biodiversity in farmland landscapes is thus necessary but complex, as species living in farmland are dependent of human-made habitats, and are thus very likely to be affected by changes in management practices driven by socio-economic changes occurring through time (Donald *et al.* 2001). Preserving biodiversity-beneficial farmland practices potentially carries both economic and social costs, and the need to balance the conflicting requirements of biodiversity, social change, and agricultural and economic development (Hinsley & Gillings 2012). Understanding the factors affecting biodiversity in agricultural landscapes is thus an increasingly important issue in conservation biology, and raises a number of questions concerning enhancement of conservation outcomes within farmlands in Europe and elsewhere: What is the effectiveness of conservation funding on farmland?; What landscape components need to be considered when managing farmland for conservation? What diversity measures should be used to inform farmland conservation management?

1.2.1 The European biodiversity conservation policy

Protected areas are essential for biodiversity conservation (Margules & Pressey 2000, Geldmann et al. 2013) and are a crucial piece for achieving the Aichi Biodiversity Targets. Natura 2000 is one of the largest networks of protected areas worldwide, and the most representative network of protected areas in Europe (Maiorano *et al.* 2015). The network was established under the Habitats Directive (92/43/EEC) in 1992, and has been the cornerstone of nature and biodiversity policy of the European Union since then (EC 2013a). It comprises Special Areas of Conservation (SAC), which include habitats and species listed in the Annexes I and II of the Habitats Directive, respectively, and Special Protection Areas (SPA), which include bird species listed on the Annex I of the Birds Directive (79/409/EEC). The designation of each protected area within the network is proposed by each member state, aiming to ensure that all habitats and species of Community interest are maintained or restored to Favourable Conservation Status in the European Union.

Natura 2000 protection areas are not strictly protected areas where all activities are systematically excluded. Instead they are mostly privately owned, and conservation management is largely implemented by landowners (EC 2014). Establishing and managing these areas thus has costs to society, either directly through funding mechanisms, or indirectly through eventual opportunity costs of foregone food

production and other economic activities (Gantioler *et al.* 2010; EC 2014). The LIFE-Nature programme (LIFE) is one of the main and cost-effective schemes, which funds best practice and demonstration projects targeting highly threatened species and habitats (EC 2010). This scheme has strategic importance for Natura 2000 because it was specifically designed to support Natura 2000 by funding very specific and targeted conservation measures in all protection areas (Gantioler *et al.* 2010; Kettunen *et al.* 2011).

1.2.2 Linking nature conservation and agricultural policies

Farmland protection areas represent about 40% of the total area included in Natura 2000 and support 255 species and 57 habitat types of Community interest closely associated with agriculture (EC 2014), including many species of conservation concern (BirdLife International 2004; Kleijn *et al.* 2011). These High Nature Value farmlands are mostly associated with low-income farm structures and farming practices, thus requiring additional funding to support farmers to maintain their low-production management practices. Funding Natura 2000 farmland is thus crucial to ensure that all habitats and species of Community interest are maintained or restored to Favourable Conservation Status in the European Union (Gantioler *et al.* 2010, EC 2014).

Despite its main focus on agricultural production, the Common Agriculture Policy (CAP) represents one of the most important European Union's funding programs affecting the management of Natura 2000 farmland. The CAP was implemented in 1962 aiming to "provide affordable food for EU citizens and a fair standard of living for farmers". However, since its initial implementation, the funding policy of the CAP led to large scale agriculture intensification, which contributed to over-production, budget problems and environmental degradation, and thus led to a strong decline of farmland biodiversity in Europe (Henle *et al*. 2008; Carvaleiro *et al*. 2013; Pe'er *et al.* 2014). Some measures such as voluntary set-aside programmes were introduced in response to these problems in the 1980's, but only with the CAP reform of 1992 was an effective environmental politic implemented. With this reform, the CAP became divided into two Pillars: "Pillar 1", under which farmers were supported to maintain incomes fully funded by the CAP budget, and "Pillar 2", designed to support Rural Development co-funded by member states, and where agri-environment schemes (AES) were included. AES aimed to provide funds for farmers to promote biodiversity conservation on their land, and represents one of the main available mechanisms to mitigate impacts of agriculture intensification and prevent or reduce declines in farmland biodiversity in Europe, both within and outside of the then-recently established Natura 2000 (Vickery *et al.* 2004; EC 2014). However, because adherence to AES schemes are periodic and voluntary, the success of these funding

schemes is largely dependent on other agricultural policies, which may provide more attractive production incentives to farmers, and may even counteract conservation objectives (Reino *et al.* 2010).

Since 1992, the Pillar 2 – AES of the CAP remained mostly unchanged, and subsequent reforms were mainly focused on the Pillar 1 – Direct Payments. The reform of the CAP of 2003 was marked by the decoupling of payments from production (i.e. farmers were no longer required to maintain production for receiving payments, as long as they keep land in good environmental and agricultural conditions), with the direct payments from Pillar 1 being replaced by the Single Farm Payment (Renwick *et al.* 2008, Brady *et al.* 2009). As many anticipated (Oñate *et al.* 2007, Tranter *et al.* 2007), the decoupling of payments from production promoted the abandonment of low-income farming systems in some areas (e.g. Ribeiro *et al.* 2014), with negative effects on some farmland species of high conservation concern (e.g. Reino *et al.* 2010). With the following reform of CAP of 2013, the Pillar 1 – direct payments became "Greening" as it for the first time incorporated the EU agri-environmental policy "for the benefit of the environment and the climate." This policy conditioned 30% of direct payments to farmers from Pillar 1 on compliance with three "greening measures," which are presently mandatory across the EU, and include (1) dedicating 5% of the arable land to Ecological Focus Areas, (2) crop diversification on farms with >15 ha of arable land, and (3) the maintenance of existing permanent grasslands (EC 2013b,c). The effectiveness of this new funding in protecting farmland biodiversity and agroecosystems may be limited, however, due to poorly specified conservation objectives and low effectiveness of mandatory commitments (Pe'er *et al*. 2014).

Many Natura 2000 protection areas have long-term funding combining LIFE with CAP funding schemes, which together with legal regulations specific to each protection area are expected to have strong positive conservation outcomes, although confirmative quantitative data are generally lacking (Hochkirch *et al.* 2013). The effectiveness of conservation investments in these areas is poorly understood because studies are scarce, and they tend to be geographically biased, short-term, and rarely consider interactions between various regulatory and funding mechanisms. For instance, LIFE seems to be one of the most effective EU conservation investments (EC 2010), but only a few long-term studies have demonstrated positive population trends of the targeted species (Pinto *et al.* 2005, Catry *et al.* 2009, Bretagnolle *et al.* 2011). Furthermore, these studies have focused on single species, and so it is uncertain whether there were wider benefits on Natura 2000 biodiversity (Devictor *et al.* 2007). In contrast, evaluations of AES ranged from single species to community level studies, and suggested that they often have null or minor positive effects on biodiversity (Kleijn *et al.* 2011, Concepción *et*

al. 2012). However, most studies have been short-term, focusing primarily on central and northern European regions, and not considering specifically the application of CAP funding schemes within Natura 2000 (Batáry *et al.* 2011a, Tryjanowski *et al.* 2011). Clearly, further information is needed on the effectiveness of long-term conservation investment in Natura 2000, particularly where there is a combination of protection regulations, LIFE projects, and CAP funding schemes, which might be expected to yield strongly positive biodiversity conservation outcomes.

1.2.3 The identification of ecologically relevant measures

1.2.3.1 Landscape components affecting biodiversity

The amount (composition), the spatial arrangement (configurational heterogeneity), and the diversity (compositional heterogeneity) of the natural and production components, shape the species and assemblages present across the landscape. The natural and semi-natural habitats (e.g., hedgerows, scrublands, riparian vegetation, woodlands, and ponds) provide key habitats for plants and animals (Ricketts 2001; Wethered & Lawes 2003), and they may act as corridors or stepping stones that facilitate dispersal among more natural areas (Hinsley & Bellamy 2000; Fischer & Lindenmayer 2002). Different crop types (e.g. arable crops, grazed lands, and orchards) with different structural characteristics and associated with distinct agricultural practices strongly influence farmland biodiversity particularly those species associated with crop habitats (Stoate *et al.* 2009; Ribeiro *et al.* 2016). Moreover, a complex spatial arrangement of cover types will increase the length of ecotones and interspersion/juxtaposition of habitats, which are favourable for many species (Tryjanowski 1999; Fahrig *et al.* 2011), and thus increased biodiversity is also expected under high configurational heterogeneity. Likewise, compositional heterogeneity is expected to be positive for farmland biodiversity as a variety of different habitats (both natural and production) may increase conditions for a larger number of species with contrasting ecological requirements, thus generating higher species richness (Pickett & Siriwardena 2011; Stein *et al.* 2014). Finally, high diversity of cover types may favour the persistence of species that use different habitats during their life cycle or throughout the year (Chamberlain *et al.* 1999; Benton *et al.* 2003).

High biodiversity levels are usually found in farmland landscapes dominated by traditional low intensity mixed farming systems that create a complex matrix of productive fields, interspersed by the remaining natural or semi-natural habitats. However, the complexity of some of these landscapes has been reduced due to agricultural intensification, which has been pointed to as a dominant driver of farmland biodiversity decline (Benton *et al.* 2003). Agriculture intensification contributes to the spatial

simplification of a mosaic landscape (i.e. landscape homogenization) by increasing farm and field sizes, removing many remaining fragments of semi-natural habitat, and promoting large-scale monoculture, aiming to increase the proportion of primary production available for human consumption and maximizing yields (Benton *et al.* 2003; Bignal & McCrachken 2000; Hinsley & Gillings 2012). Also, simplification of crop rotations causes temporal landscape homogenization because continuous cropping and loss of ley grassland and fallowed land means that fields remain under similar agriculturally productive management for longer continuous periods (Robinson & Sutherland 2002; Benton *et al.* 2003).

Restoring heterogeneity may thus be particularly important for biodiversity in landscapes dominated by vast areas of intensively managed structurally simple monocultures, where the proportion of land occupied by the production component is large, and the cover by native vegetation is small or poorly connected (Mayfield & Daily 2005; Fischer *et al*. 2005; Benton *et al*. 2003; Fischer *et al.* 2006). Heterogeneous landscapes may resemble natural patterns providing greater biodiversity benefits than simplified landscapes (Benton *et al*. 2003; Mayfield & Daily 2005; Fischer *et al.* 2006, Fahrig *et al.* 2011). However, in some cases increasing heterogeneity may result in further habitat fragmentation, with harmful consequences to the original biodiversity (Fahrig 2003; Báldi & Batáry 2011). This may occur because the original landscapes may have been more homogeneous than the modern systems that have replaced them (Báldi & Batáry 2011). This may be the case in semi-natural open grassland systems where grassland specialist species, which nest and forage on the ground, tend to prefer homogeneous landscapes and may avoid heterogeneous farmland (e.g. Morgado *et al*. 2010; Reino *et al*. 2010; Silva *et al*. 2010).

Managing farmland landscapes for biodiversity conservation thus requires the identification of the components that shape biodiversity across the landscape in order to define the best strategies to mitigate the effects of agriculture intensification and increase biodiversity. Common approaches to increase biodiversity within farmland involve improving the natural component of the landscape by increasing the amount of natural and semi-natural habitats, or improving the production component of the landscape by increasing the amount of biodiversity-friendly crops. However, because both these approaches may negatively impact economic output, an alternative might be to enhance both compositional and configurational heterogeneity of the landscape, without necessarily changing composition (Fahrig *et al.* 2011). While managing landscape heterogeneity may provide a valuable framework for improving biodiversity conservation on farmland without reducing yields (Batáry *et al.* 2011b; Concepción *et al.* 2012), its practical application in real landscapes requires further information on the relative

importance of landscape composition versus heterogeneity, as well as on the relative role of the different heterogeneity components of both the natural and production cover types to biodiversity patterns.

1.2.3.2 Selecting diversity metrics to inform conservation actions

Whittaker (1960) identified three levels of species diversity, each representing different scales. The number of species present in a region (i.e., gamma diversity, γ) is shaped by both the richness of species of each particular site (i.e. alpha diversity, α), and how species are distributed across the region (i.e. beta diversity, β) (Whittaker 1960, 1972). α-diversity is a local diversity metric, and is the primary, the simplest, and the most common way to measure species diversity as it is based on the number of species sampled in each sampling site (Whittaker 1960). β-diversity reflects the extent of change of assemblage composition, or degree of assemblage differentiation, in relation to the landscape heterogeneity, and may be estimated by a number of dissimilarity indices between sampling sites (Whittaker 1972, see Koleff *et al.* 2003 for a review). Finally, γ-diversity is a regional diversity metric, and may be directly estimated by combining all alpha samples for a given region, provided sampling is representative of the regional landscape heterogeneity (Whittaker 1960). Although α-diversity is the most common metric to assess the effects of human activities on biodiversity (Newbold *et al.* 2015), the usage of this simplistic measure may mask crucial information such as the influence of land use changes on species distributions across the landscape, which is given by β-diversity.

β-diversity may thus be particularly important to design or evaluate specific conservation actions on farmland where the diversity and spatial arrangement of habitats (i.e. landscape heterogeneity) are widely recognised as key for biodiversity conservation (Benton *et al.* 2003; Fahrig *et al.* 2011; but see Báldi & Batáry 2011), though their actual biodiversity benefits remain disputed (Stoate *et al.* 2009; Batáry *et al.* 2015). A few studies have used β-diversity to address these issues, providing evidence that β-diversity was lower in intensive than in extensive farmland (Ekroos *et al.* 2010; Flohre *et al.* 2011; Karp *et al.* 2012), and in conventional than in organic farms (Gabriel *et al.* 2006; Clough *et al.* 2007), though the patterns observed varied across spatial scales, taxa and functional groups. A frequent pattern in low intensity farmland landscapes is that alpha diversity is not always very high but β- and γ-diversity are generally quite high because of the high heterogeneity of the landscape (Blondel & Aronson 1999). Conversely, in high-intensity farmland landscapes, where the landscape is expected to be homogeneous due to the dominance of large monoculture production fields, gamma diversity is expected to be low due to both low α- and β-diversity. The dissimilarities

across sites may result from two different ecological processes: species replacement (β_{Rep}) and species richness difference ($\beta_{RichDiff}$) (Harrison *et al.* 1992; Williams 1996; Lennon *et al.* 2001; Legendre 2014). β_{Rep} and $\beta_{RichDiff}$ may be assessed by the additive decomposition of Jaccard or Sørensen pairwise dissimilarity indices (Legendre 2014). Specifically, β_{Rep} reflects dissimilarities among assemblages across the landscape mainly driven by differences in the species compositions of each site. It is also called turnover when analysed along spatial or environmental gradients (Legendre *et al.* 2014). $\beta_{RichDiff}$ reflects dissimilarities based on the number of species, i.e. some sites include a larger number of species than others (Legendre 2014). A particular case of richness difference is when the species at a site are a strict subset of the species at a richer site, which is called nestedness (Baselga, 2012; Legendre et al. 2014).

Examining trends in β-diversity may thus be useful to understand the impacts of anthropogenic drivers whose effects on γ-diversity may not be adequately captured by α-diversity alone (Socolar *et al.* 2016). For instance, land-use changes increasing habitat diversity may increase β-diversity due to species replacement among sites with different habitats (i.e. the replacement component of β-diversity, β_{Repl}; Legendre 2014), and thus increase γ-diversity without necessarily changing the average number of species observed at a sampling site, α-diversity (Gaston *et al.* 2007; Monnet *et al.* 2014). Alternatively, land-use changes affecting habitat attributes may cause variation in the number of species among sites with different habitat characteristics (i.e. the richness difference component of β-diversity, $\beta_{RichDiff}$; Legendre 2014), without necessarily affecting β_{Repl}. In this case, the contribution of β-diversity to γ-diversity will likely be relatively small, and local or sampling site-specific factors affecting α-diversity may be particularly relevant. There is thus a need to consider β-diversity and its components, β_{Repl} and $\beta_{RichDiff}$, in conservation research to understand biodiversity changes and their underlying ecological mechanisms (Socolar *et al.* 2016; Żmihorski *et al.* 2016).

1.3 The model system: the Mediterranean farmland birds of southern Portugal

1.3.1 The biological context

Among the vertebrates, birds are considered a particularly suitable taxonomic group for addressing questions regarding biodiversity conservation on farmland. This may be partially explained because birds are easy to study, so one may obtain a large amount of information during a short time, and over long time periods (e.g. Jørgensen *et al.* 2016). Moreover their ecology is well known (Wiens 1989a,b). Birds occur in a wide range of habitats, showing different degrees of species-habitat specialization within the

farmland landscape, and thus different degrees of response to agricultural management that shapes landscape features (Devictor *et al.* 2010). As a result, birds have been used in many studies to identify the consequences of agriculture intensification for biodiversity, where huge population declines and range retractions of many bird species living in farmland have been reported (Krebs *et al.* 1999; Donald *et al.* 2001; Wilson *et al.* 2009).

This thesis focused on breeding bird assemblages living on Euro-Mediterranean farmlands. Bird assemblages in these farmlands are highly diverse and primary shaped by the biogeographic origin, climate, and human-management history of the region (Covas & Blondel 1998). The high biodiversity levels usually found in these historically human-modified landscapes are supported by the mosaic landscape of natural and crop habitats that supply contrasting foraging, nesting and sheltering habitats for many bird species with different habitat requirements (Blondel & Aronson 1999). However, existing farmland habitats are generally poorer than those in non-disturbed areas (Hinsley & Gillings 2012), so that many bird species living on farmlands may need to use more than one habitat type to satisfy their requirements (Dunning *et al.* 1992). Species-habitat relationships in farmland may thus deviate from those observed in more natural landscapes, and those relations are expected to be different depending on the composition and structure of the farmland landscape (Hinsley & Gillings 2012). The categorization of bird assemblages reflecting species-habitat relationships may thus be a very useful way to identify the effects of agricultural management in line with specific conservation objectives, though it would require previous knowledge on the species-habitat relationships within the target farmland region (Devictor *et al.* 2010).

In this thesis knowledge acquired during the last two decades in Mediterranean farmland, and particularly in the Iberian cereal-steppe habitats (e.g. Moreira & Leitão 1996; Suárez *et al.* 1997; Moreira 1999; Delgado & Moreira 2000; Pinto *et al.* 2005; Moreira *et al.* 2005; Equipa Atlas 2008; Morgado *et al.* 2010; Reino *et al.* 2009, 2010; Leitão *et al.* 2010; Moreira *et al.* 2012) was used to classify bird species within the broad categories ‘farmland birds’ versus ‘woodland birds’ adopted by the European Bird Census Council (EBCC 2012) to characterize species-habitat relationships within farmland. The ‘farmland birds’ assemblage comprised all the species associated with all farmland habitats including arable fields, permanent crops, and hedgerows. This assemblage includes species that use several habitats within the farmland for different purposes, such as feeding, breeding and shelter (e.g. white stork *Ciconia ciconia,* stonechat *Saxicola rubicola,* spotless starling *Sturnus unicolor,* goldfinch *Carduelis carduelis*), and species that have become specialized on one or more crop habitat type (‘farmland specialists’) (Dunning *et al.* 1992; Devictor *et al.* 2010).

Farmland specialists are particularly vulnerable to agricultural management as they are dependent on one or more crop habitats from the landscape mosaic (Devictor *et al.* 2010). This is the case of the 'ground nesting birds' (e.g. red-legged partridge *Alectoris rufa*, bee-eater *Merops apiaster*), or the 'steppe birds,' which are species that are rare or absent outside open grassland habitats (e.g. tawny pipit *Anthus campestris,* common quail *Coturnix coturnix,* Montagu's harrier *Circus pygargus,* lesser kestrel *Falco naumanni,* Iiitle bustard *Tetrax tetrax,* great bustard *Otis tarda,* black-eared wheatear *Oenanthe hispanica*, black-billed sandgrouse *Pterocles orientalis,* calandra lark *Melanocorypha calandra,* great short-toed lark *Calandrella brachydactyla,* crested lark *Galerida cristata* and Thekla lark *G. theklae,* zitting cisticola *Cisticola juncidis* and corn bunting *Emberiza calandra*). Steppe bird specialists may be grouped into different assemblages reflecting preferred association with different elements of the traditional farmland mosaic (i.e., fallow [calandra lark, and little bustard], cereal [Montagu's harrier, zitting cisticola, common quail, corn bunting], and ploughed fields [tawny pipit *Anthus campestris*, stone curlew *Burhinus oedicnemus*, great short-toed lark, black-eared wheatear, black-billed sandgrouse], Delgado & Moreira 2000, Leitão *et al.* 2010). Many of these species are threatened and charismatic species such as the little and great bustards, which are flagship species of the traditionally cereal steppes of Iberian Peninsula, and that have been the focus of many conservation actions such as LIFE-Nature programs (see http://ec.europa.eu/environment/life/project/Projects/).

The 'woodland birds' assemblage includes all bird species living within the farmland that depend on woodland and/or shrubland habitat patches for feeding and breeding. This assemblage includes typical Mediterranean birds that are primarily associated with herbaceous and shrubland habitats (e.g. common nightingale *Luscinia megarhynchos,* Cetti's warbler *Cettia cetti,* Sardinian warbler *Sylvia melanocephala*), and forest specialists (e.g. great spotted woodpecker *Dendrocopos major,* woodlark *Lullula arborea,* blue tit *Cyanistes caeruleus,* great tit *Parus major,* chaffinch *Fringilla coelebs*, short-toed treecreeper *Certhia brachydactyla*), which are widespread and abundant across Europe (Covas & Blondel 1998; Suárez-Seoane *et al.* 2002). In open farmland this assemblage is usually associated with natural components of the landscape, and thus these species are expected to benefit from traditional low-intensity farming systems where woodlands, shrublands, riparian vegetation, hedgerows are more likely to occur, in oak agro-forest-pasture farming systems and abandoned fields with early successional vegetation stages (Santana *et al.* 2012), or even in some traditional orchards such as olive groves and almonds (Covas & Blondel 1998).

1.3.2 The study area

The study area comprised the Mediterranean open farmland region of southern Portugal that is representative of Iberian cereal steppes, and holds internationally important populations of bird species of conservation concern (BirdLife International 2004). The region has a gently undulating landscape (100–300 m a.s.l.), and is in the meso-Mediterranean bioclimatic zone (Rivas-Martinez 1981), with hot summers, mild winters, and with >75% of annual rainfall from October to March (SNIRH, National System of Water Resources Information database). The study focused in the Special Protection Area (SPA) of Castro Verde (37º 41´ N, 8º 00´ W), which is a Natura 2000 site designed to protect steppe birds and their habitats, and the nearby high-intensity farmland (about 10 km north) of Ferreira do Alentejo (38º 03´ N, 8º 06´ W).

The SPA of Castro Verde was dominated for decades by a traditional farming system characterised by the rotation of rain-fed cereals and fallows typically grazed by sheep (Figure 1.2), which provides habitat for steppe bird populations of conservation concern (Delgado & Moreira 2000). The southern part of the SPA includes a mosaic of shrubland interspersed with old fallows resulting from agricultural abandonment and scrub encroachment (Moreira *et al.* 2005), and some parts of the area are afforested with eucalyptus (*Eucalyptus* sp.), pine (*Pinus* sp.), and oak (*Q. suber* and *Q. rotundifolia*) plantations, sometimes also grazed by sheep (see Reino *et al.* 2009) (Fig. 1.2). To preserve the traditional farming system, an agri-environment scheme was established in 1995 and the SPA of Castro Verde was designated in 1999, which comprised legal restrictions to afforestation, the development of irrigation infrastructures, and the expansion of permanent crops (Ribeiro *et al.* 2014). Furthermore, there were several LIFE-Nature conservation projects targeting mainly great and little bustards and lesser kestrel (see http://ec.europa.eu/environment/life/project/Projects/), which included the purchase and management of critical areas, and the improvement of breeding and foraging habitats (Pinto *et al.* 2005; Catry *et al.* 2009; Moreira *et al.* 2012). Despite these efforts, over the last decade there were marked shifts from the traditional system towards the specialized production of either cattle or sheep, with declines in cereal and fallow land, and increases in permanent pastures (Ribeiro *et al.* 2014). This probably resulted from the decoupling of payments from production introduced by the CAP reform of 2003 (i.e. farmers were no longer required to maintain production for receiving CAP payments), as arable crops were completely decoupled while sheep and suckler cows remained partially and fully coupled, respectively (Ribeiro *et al.* 2014).

The high-intensity farmland of Ferreira do Alentejo contrasted markedly with the SPA, because it smaller fields, less fallow land, irrigation infrastructures, and thus mainly produced irrigated rather than rain-fed annual crops, more productive soils with a high

proportion of cultivated land, and no constraints to crop conversion (Ribeiro *et al.* 2014). The main change in agricultural farming systems in high-intensity farmland was the shift from arable to permanent crops (mainly olive groves) (Ribeiro *et al.* 2014).

Fig. 1.2 – Photographs showing the main agricultural habitats in the study area. (a) the low-intensity farmland landscape mosaic, photo by Pedro Beja; (b) high-intensity olive grove; (c) initial stage of a rain-fed cereal field; (d) fallow/pasture field; (e,g) pastures grazed by sheep, photos by Norbert Sauberer; (f) pasture grazed by cattle, photo by Ana Júlia Pereira; (h) traditional olive grove grazed by sheep, photo by Rui Morgado.

1.4 Objectives

This thesis focused on biodiversity conservation in Euro-Mediterranean farmlands, which are of general relevance for global biodiversity conservation, by using Mediterranean farmland birds of southern Portugal as a model system. Its main aim was to contribute to a more complete understanding of how different aspects of biological diversity (e.g. local and regional species richness and variations in assemblage composition) vary in space and time in relation to conservation actions (i.e. protection regulations, agri-environmental measures, conservation research and projects); socioecological constrains (e.g. agricultural policies, market decisions, farmers decisions, biophysical conditions); and landscape characteristics (e.g. landscape composition, compositional heterogeneity and configurational heterogeneity of the natural and production habitats), and how these relations may contribute to inform and evaluate conservation actions on farmland (Fig. 1.3). In this context, the following research objectives were identified:

1) To determine the effectiveness of conservation investment in farmland;
2) To identify the landscape features affecting biodiversity trends;
3) To identify the value of different diversity metrics to inform agricultural policies and conservation actions;
4) To provide insights for the design, manage and evaluation of conservation actions on farmland.

To achieve these goals we used a network of 78 250-m transects covering the SPA of Castro Verde (46), and the nearby high-intensity farmland area of Ferreira do Alentejo (32), where breeding birds were sampled annually before (1995-1997) and after (2010-2012) the Common Agricultural Policy reform of 2003. For each period, the land cover and land uses were mapped within 250-m buffers around each transect.

1.5 Thesis structure

The thesis is organized into five chapters. **Chapter 1** provides a review of the current knowledge on biodiversity conservation and the main challenges on this topic applied to farmland landscapes that this thesis proposes to answer. Chapters 2 to 4 comprise three scientific manuscripts published in peer-reviewed journals (Fig. 1.3) where each objective outlined above is addressed.

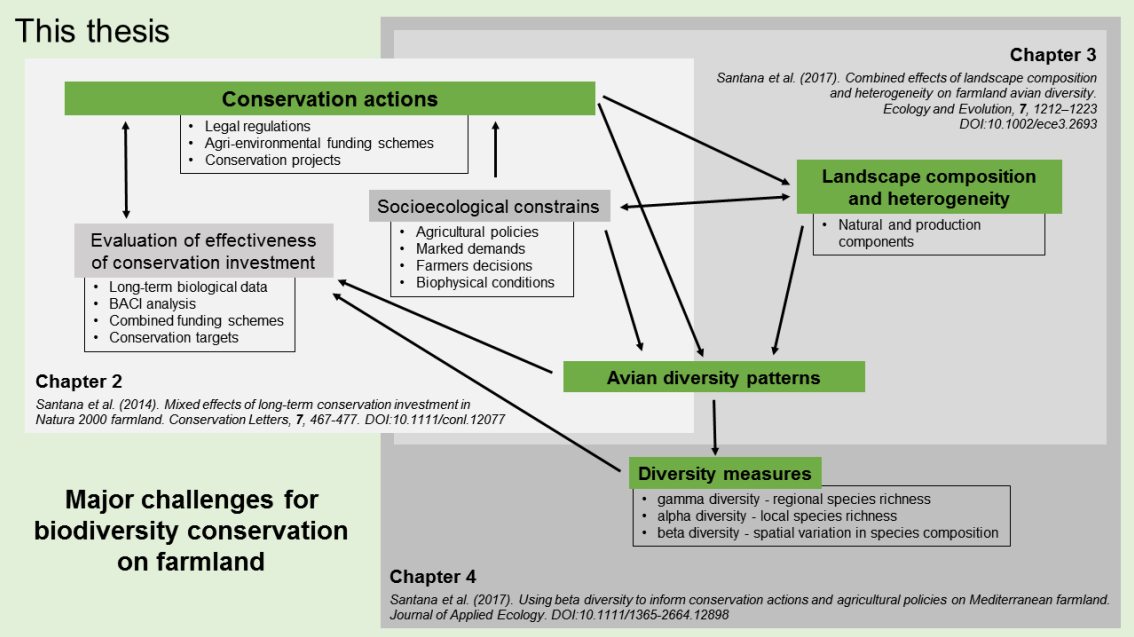

Fig. 1.3 – Thesis structure showing the conceptual relations among the case studies presented on Chapters 2, 3 and 4, and how they jointly may contribute to inform and evaluate biodiversity conservation actions on farmland landscapes.

In **Chapter 2** (Santana *et al.* 2014), the effects of long-term conservation investment in Natura 2000 farmland are evaluated. To achieve this, the effects of protection regulations, conservation projects, and agri-environment schemes in a farmland bird protection area (Castro Verde SPA) encompassing a period of 17 years, on the trends in bird assemblages' species richness and abundance, are evaluated. Trends in the SPA were compared to those in a nearby high-intensity farmland of Ferreira do Alentejo without conservation investment, which was used as a control. Bird assemblages were selected to reflect the degree of specialization in open farmland habitats that were the focus of conservation actions and conservation status. The results obtained were used to discuss the design and evaluation of conservation actions on farmland.

In **Chapter 3** (Santana *et al.* 2017a), the combined effects of managing landscape composition and heterogeneity to achieve conservation benefits on farmland biodiversity are examined. To achieve this, the effects of composition and compositional and configurational heterogeneity of both the natural and production components of the landscape (*sensu* Fahrig *et al.* 2011), on spatial and temporal trends in species richness of breeding bird assemblages reflecting species-habitat association in open Mediterranean farmland, are analysed. The results obtained were used to discuss the importance of each landscape component when managing farmlands for conservation, and how this importance may vary widely in relation to conservation objectives.

In **Chapter 4** (Santana *et al.* 2017b), the value of β-diversity to inform agricultural policies and conservation actions on Mediterranean farmland is evaluated. To achieve

this, the contribution of α- and β-diversity to γ-diversity variation in low- and high-intensity Mediterranean farmland, before (1995-1997) and after (2010-2012) the CAP reform of 2003 were quantified to assess the value of β-diversity to guide conservation on farmland. Additionally, β-diversity was related to landscape heterogeneity to assess the conservation significance of β-diversity changes. Results were used to discuss the value and limitations of beta diversity to inform conservation management.

In **Chapter 5** the main conclusions from these studies, and general guidelines to design and evaluate conservation actions on farmland, and particularly to manage bird diversity on open Mediterranean farmland, as well as some future research prospects, are presented.

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Chapter 2

Mixed effects of long-term conservation investment in Natura 2000 farmland

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2. Mixed effects of long-term conservation investment in Natura 2000 farmland

2.1 Abstract

1. Evaluating the effectiveness of conservation funding is crucial for correct allocation of limited resources.

2. Here we used bird monitoring data to assess the effects of long-term conservation investment in a Natura 2000 (N2000) bird protection area (PA), which during two decades benefited from protection regulations, conservation projects, and agri-environment schemes.

3. Variation between 1995-1997 and 2010-2012 in richness and abundance of flagship (*Otis tarda*, *Tetrax tetrax*, and *Falco naumanni*) and specialized fallow field species were more favorable (i.e., increased more or declined less) inside the PA than in a nearby control area. However, the reverse was found for total bird species, farmland, ground-nesting and steppe species, species associated to ploughed fields, and species of European conservation concern.

4. *Synthesis and applications*. Enhancing the effectiveness of conservation investment in N2000 farmland may require a greater focus on the wider biodiversity alongside that currently devoted to flagship species, as well as improved matching between conservation and agricultural policies.

2.2 Introduction

The Natura 2000 (N2000) network comprises Special Protection Areas (SPA; Directive 79/409/EEC) and Special Areas of Conservation (Directive 92/43/EEC), and is the centerpiece of European Union (EU) nature and biodiversity policy (EC 2013). Most N2000 land is privately owned, consequently establishing and managing Protection Areas (PA) involves considerable conservation investment, part of which has been supported by EU financing mechanisms (EC 2013). The LIFE-Nature programme (LIFE) is one the main schemes, funding best practice and demonstration projects targeting highly threatened species and habitats (EC 2010). Agri-environment schemes (AES) are also key mechanisms providing funds for farmers to promote conservation on farmland under the Common Agriculture Policy (CAP) (Stoate *et al.* 2009). AES are particularly relevant because agriculture is the most important economic activity within European PA (EEA 2006), and extensive farmland supports many species of conservation concern (BirdLife International 2004; Kleijn *et al.* 2011). N2000 has thus major costs to society,

either directly through funding mechanisms, or indirectly through eventual opportunity costs of foregone food production and economic activities (Gantioler *et al.* 2010). Evaluating the effectiveness of conservation investments is thus considered a high priority (Kleijn *et al.* 2011; Hochkirch *et al.* 2013).

The effectiveness of EU conservation investments in N2000 is poorly understood, because studies are scarce, and they tend to be geographically biased, short-term, and rarely consider interactions between various protection and funding schemes. For instance, although protection regulations in association with long-term funding should yield positive conservation outcomes in N2000, confirmative quantitative data is generally lacking (Hochkirch *et al.* 2013). LIFE seems to be one of the most effective EU conservation investments (EC 2010), but only a few long-term studies have demonstrated positive population trends of the targeted species (Pinto *et al.* 2005; Catry *et al.* 2009; Bretagnolle *et al.* 2011). Furthermore, these studies have focused on single species, and so it is uncertain whether there were wider benefits on N2000 biodiversity (Devictor *et al.* 2007). In contrast, evaluations of AES included from single species to community level studies, suggesting that they often have null or minor positive effects on biodiversity (Kleijn *et al.* 2011; Concepción *et al.* 2012). However, most studies have been short-term, focusing primarily on central and northern European regions, and not considering specifically the application of AES within N2000 (Batáry *et al.* 2011; Tryjanowski *et al.* 2011). Clearly, further information is needed on the effectiveness of long-term conservation investment in N2000, particularly where there is a combination of protection regulations, LIFE and AES, which might be expected to yield strongly positive biodiversity conservation outcomes.

Here we provide a case study on the effectiveness of long-term conservation investment in N2000. We focused on a SPA that is representative of Iberian cereal steppes, which hold internationally important populations of bird species of conservation concern (BirdLife International 2004). Since 1993, the SPA has benefited from investments specifically targeted at bird conservation, including: (1) protection regulations restricting activities such as afforestation, expansion of perennial crops (e.g. olive groves), and building of irrigation infrastructures; (2) LIFE targeting flagship species such as *Otis tarda*, *Tetrax tetrax* and *Falco naumanni*; (3) AES designed to maintain agricultural practices beneficial to steppe birds; and 4) concentration of research projects designed to inform conservation management (Table S2.1). Specifically, we compared breeding bird assemblage trends in the SPA and in a nearby control area, using data collected in 1995-1997 and 2010-2012. We expected that trends would be most favorable (i.e., more positive or less negative) inside the SPA for: (1) overall species richness and abundance (Batáry *et al.* 2011); (2) richness and abundance of farmland

species (Guerrero *et al.* 2011), particularly of ground-nesting (Bas *et al.* 2009) and steppe (Stoate *et al.* 2000) specialists; (3) richness and abundance of groups of species associated with each element of the traditional farmland mosaic (i.e., fallow, cereal, and ploughed fields); and (4) richness and abundance of Species of European Conservation Concern (SPEC), and of flagship species that were the main targets of conservation investment (Catry *et al.* 2009; Bretagnolle *et al.* 2011). Finally, we expected that (5) farmland bird assemblage composition would be increasingly dominated by the steppe specialists. Our study has implications for the design of effective AES and other schemes funding conservation on farmland, which are of general relevance for biodiversity conservation both in Europe and elsewhere (Attwod *et al.* 2009; Kleijn *et al.* 2011).

2.3 Methods

2.3.1 Study area

The study was conducted in Portugal, in the SPA of Castro Verde and in a control area without conservation investment (Fig. 2.1). The landscape is gently undulating (100-300 m a.s.l.), and climate is Mediterranean, with hot summers, mild winters, and >75% of annual rainfall in October–March. The SPA was dominated for decades by traditional rotation of dry cereals and fallows typically grazed by sheep (Delgado & Moreira 2000), but permanent pastures and cattle stocking increased in recent years, along with declines in cereals, fallows, and sheep stocking (Table S2.2). The control was selected because it was the most comparable farmland area close to the SPA (ca. 10-km), showing overall similarities in dominant land uses at the beginning of the study, though it had smaller farms, less fallow land and more irrigable area (Table S2.2). In recent years, perennial crops (mainly olive groves) increased at the expenses of cereals (Table S2.2).

2.3.2 Bird data

Birds were sampled using a network of transects set in 1995 (Stoate *et al.* 2000). Specifically, a 1-km grid was overlaid on the study area, and grid intersections were selected randomly both within the SPA (46) and the control (32). One 250-m transect following a random bearing started at each grid intersection. Birds were counted annually once in each transect in April-May, in 1995-1997 and 2010-2012. Occasionally, some transects could not be counted in a given year due to logistic constraints (counts per transect=5.7±0.6 SD; Table S2.3). Transects were walked in early morning and late afternoon, and birds seen or heard within 250-m bands were identified and counted. A large searching radius was used to increase detection rate of shy species such as

bustards. Although this may have contributed to underestimate relative abundance of small songbirds with low detectability at far distance, this should not have introduced any serious bias, because detectability was high in open farmland habitats, the procedure was consistent across years and sampling areas, and we were interested in temporal trends rather than on relative abundances at any particular time. Aquatic birds were excluded because they are unlikely to respond directly to farmland management and they were inadequately sampled by our approach.

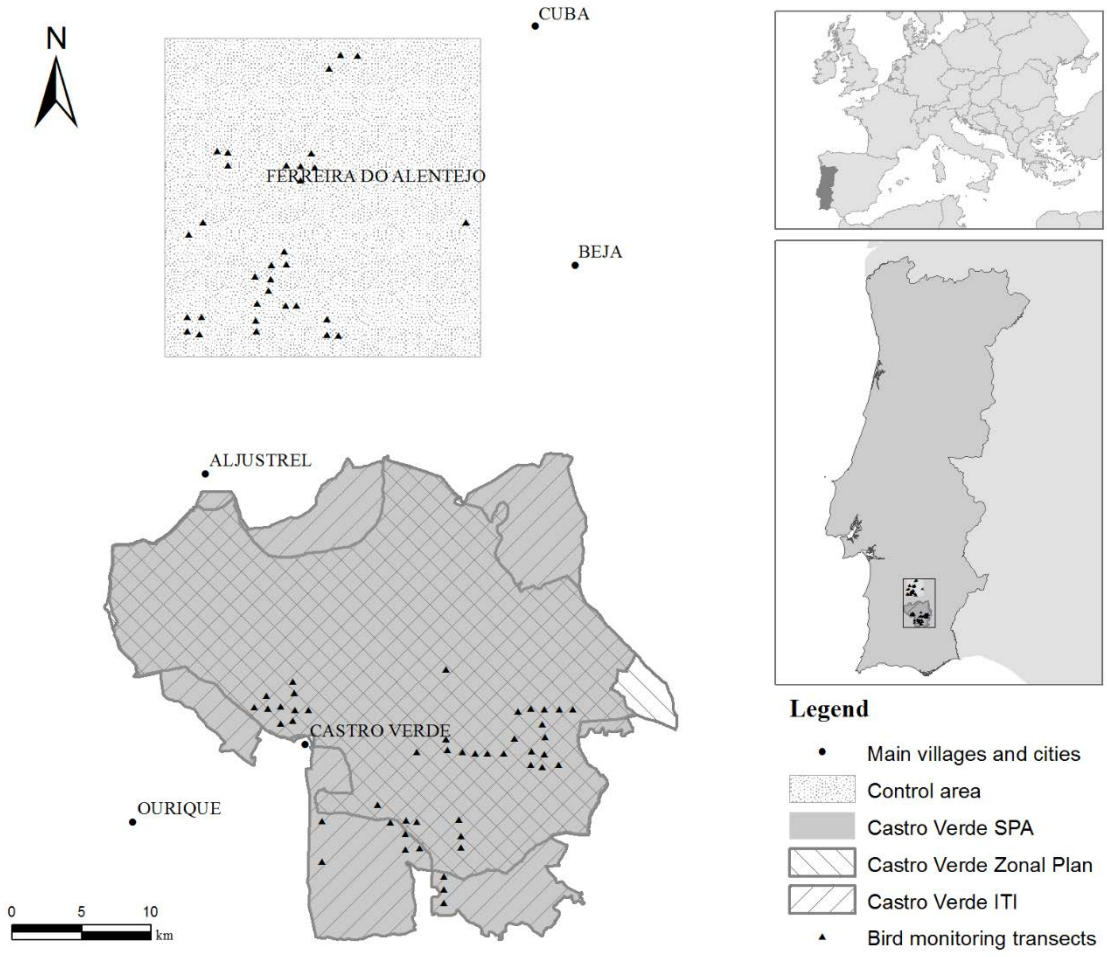

Fig. 2.1 - Location of the study area in southern Portugal, showing transects sampled for breeding birds within the Castro Verde SPA (n=46) and the nearby control area (n=32). Areas of implementation of the targeted agri-environment schemes designed for steppe birds conservation are also shown: the Castro Verde Zonal Plan (1995-2006) and the Integrated Territorial Intervention (ITI, 2007-2013).

Bird species were categorized to aid interpretation of ecological effects (Table S2.4). We considered groups reflecting the degree of specialization in open farmland habitats that were the focus of conservation investment: i) farmland - species associated with all farmland habitat types (e.g. arable fields, perennial crops, hedgerows); ii) ground-nesting - species nesting on the ground; and iii) steppe - species that are rare or absent outside

open grassland habitats. Steppe birds were further grouped according to their associations with elements of the traditional farmland mosaic (i.e., fallow, cereal and ploughed fields; Delgado & Moreira 2000), aiming to identify possible changes reflecting fine modifications in agricultural practices. A group of species with unfavorable conservation status in Europe (SPEC 1-3; BirdLife International 2004) was used to estimate the overall effects on species of conservation concern. Finally, we used a group of flagship species because they are globally threatened and they were the main targets of conservation investment (Table S2.1).

2.3.3 Analyses

We tested the general hypothesis that temporal bird trends within the SPA were more favorable (i.e. more positive or less negative) than in the control, using a procedure akin to a BACI (Before-After-Control-Impact) design with multiple sites and years (Smith 2006). We modeled species richness (number of species per transect) and abundance (number of birds per transect) against farmland type (SPA versus control), sampling period (1995-97 versus 2010-12), and their interaction (Table 2.1). The main interest was on the interaction term, which indicated whether the trend observed in the SPA was above (positive coefficient) or below (negative coefficient) that expected from the trend observed in the control.

Table 2.1 - Fixed component of the alternative GLMM candidate models used for model inference, and corresponding ecological effects. SC = SPA *vs*. control area; BA = 1995-97 vs. 2010-2012.

Alternative models		**Ecological effects**
H_1	$g_1 = \beta_0$	No effects (null model)
H_2	$g_2 = \beta_0 + \beta_1 (SC)$	Farmland type
H_3	$g_3 = \beta_0 + \beta_1 (BA)$	Period
H_4	$g_4 = \beta_0 + \beta_1 (SC) + \beta_2 (BA)$	Farmland type and period
H_5	$g_5 = \beta_0 + \beta_1 (SC) + \beta_2 (BA) + \beta_3 (SC * BA)$	Farmland type, period and interaction effects (full model)

Modeling was based on zero-inflated models with negative binomial errors, thereby accounting for excess of zeros and over-dispersion (Zuur *et al.* 2009). Generalized linear mixed models (GLMMs) were used to account for lack of independence among samples, treating transects and sampling year as random effects (Pinheiro & Bates 2000). Model building was based on the information theoretic approach, and inference was based on model averaging (Burnham & Anderson 2002). For each dependent variable we calculated: (i) model probabilities (w_i) for all five candidate models (Table 2.1), based on AIC; (ii) model average of each coefficient among models; and (iii) 95% confidence intervals (CI) for each model averaged coefficient from unconditional variances (Burnham & Anderson 2002). Dominant gradients in farmland bird assemblage

composition were extracted using principal component analysis (PCA) on the bird abundance data for all transects, excluding species with <20 overall occurrences. PC scores were then related to explanatory variables as in previous analyses, using GLMMs with Gaussian errors.

Because the categorization of bird assemblages in many groups may cause spurious relationships, we used a permutation approach to estimate the likelihood of results arising by chance (Petchey & Gaston 2006). Specifically, we compared the coefficient of the interaction term estimated for each species group with the frequency distribution of coefficients estimated using random groups of species (see Table S2.7 for methodological details). All analyses were performed using packages glmmADMB ('glmmadmb'), lme4 ('lmer'), bbmle ('AIC') and vegan ('prcomp') in R 2.15.2 (R Development Core Team 2012).

2.4. Results

2.4.1 Trends in species richness and abundance

Species richness and abundances were generally higher in the SPA than in the control, and they were higher in 2010-12 than in 1995-97 (Figs. 2.2 and 2.3, Table S2.5). In most cases there was strong support for interaction effects between farmland type and sampling period, suggesting that temporal bird trends differed between the SPA and the control (Fig. 2.4, Table S2.6). Contrary to our expectation, however, the sign of the interaction coefficient was negative in most cases, suggesting that changes in the SPA were less favorable than expected from corresponding trends in the control (Fig. 2.4, Table S2.6). This effect was particularly marked for overall species richness, with the highest values found in the SPA in 1995-97, and in the control in 2010-12 (Fig. 2.2). Tendencies were less negative for farmland, ground-nesting and steppe species, along with increasing specialization in open farmland habitats (Fig. 2.4), and this effect was moderately supported by permutation tests (percentiles: 79.4-90.2%; Table S2.7). Species associated with ploughed fields had much less favorable trends inside the SPA than in the control area (Fig. 2.4), with interaction coefficients being more negative than expected for random groups of steppe birds (percentiles: 8.8-10.5%; Table S2.7). Conversely, effects on species associated with fallows were positive (Fig. 2.4), with coefficients larger than that of random steppe groups (percentiles: 78.1-90.5%; Table S2.7). No effects were found for species associated with cereal fields (Fig. 2.4; Table S2.7).

Species of conservation concern (SPEC) had less favorable trends in the SPA than in the control (Fig. 2.4), though the interaction coefficients tended to be less

negative than that of random groups of species (percentiles: 76.3-79.1%; Table S2.7). Conversely, the effect on flagship species was positive (Fig. 2.4), with interaction coefficients more positive than expected for random sets of SPEC (percentiles: 89.0-95.2%; Table S2.7).

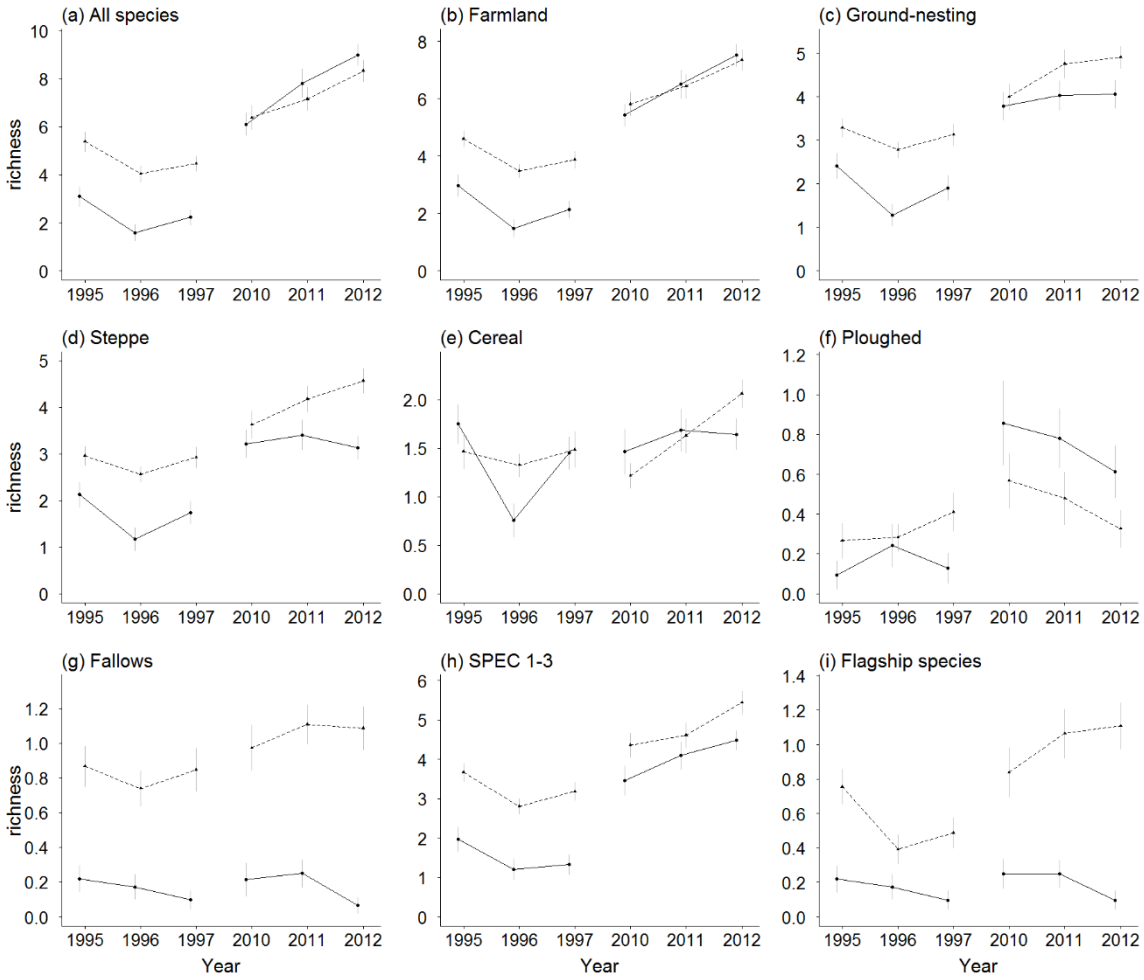

Fig. 2.2 - Temporal trends in bird species richness (mean± standard error) within the Castro Verde SPA (dotted lines) and the control area (full lines).

2.4.2 Trends in bird assemblages

Assemblage composition in the SPA and the control diverged over time (Table S2.8). Variation in the control was most pronounced along PC1 (Figure 2.5), reflecting increasing dominance by generalist farmland species (e.g., *Sturnus unicolor*, *Saxicola torquatus*, *Merops apiaster*, *Streptopelia decaocto*); variation along PC2 reflected increasing dominance of species associated with ploughed fields (e.g., *Oenanthe hispanica*, *Anthus campestris*, *Calandrella brachydactyla*). Assemblage composition in the SPA was relatively more stable, although there was a tendency for increasing dominance of species associated with cereal fields (e.g., *Cisticola juncidis*, *Emberiza*

calandra, *Coturnix coturnix, Circus pygargus*), and a decline in ploughed field species (Figure 2.5).

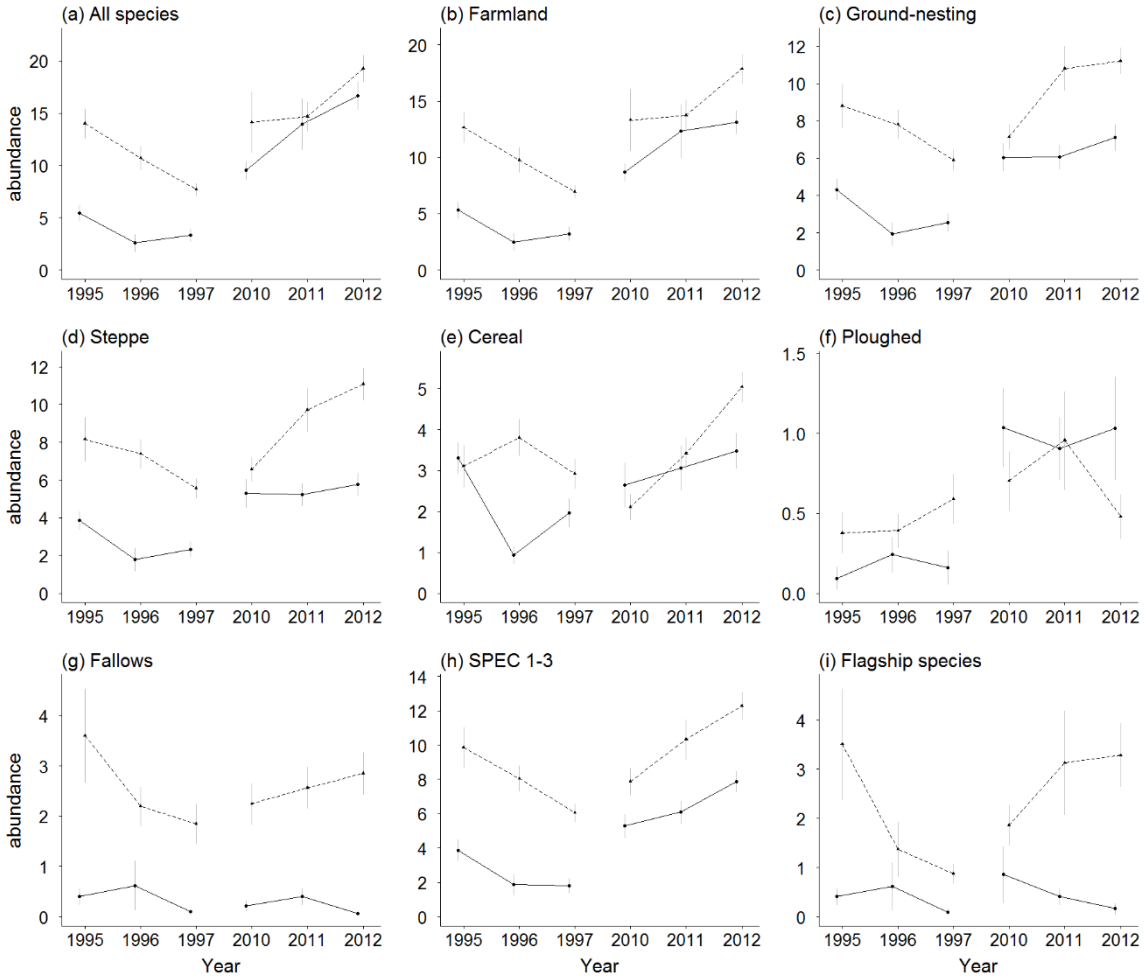

Fig. 2.3 - Temporal trends in bird abundance (mean± standard error) within the Castro Verde SPA (dotted lines) and the control area (full lines).

2.5 Discussion

Our study showed mixed effects of long-term conservation investment in Natura 2000 farmland. We found positive effects on flagship species, and on species associated with fallows, which were the main targets of conservation investment. In contrast, temporal trends in the control area appeared most favorable for the overall bird assemblage, including the farmland, ground-nesting and steppe groups of species, and even the Species of European Conservation Concern (SPEC). These patterns seem surprising, because the studied SPA benefited during two decades from protection regulations, LIFE, and AES, whereas the control was under agriculture intensification and did not receive conservation-oriented investments. Interpretation of these results, however, requires due consideration of a number of factors, including potential limitations of the

study, shortcomings of general metrics used to judge conservation success, changes in land use (Table S2.2), and the focus of conservation on a few flagship species (Table S2.1).

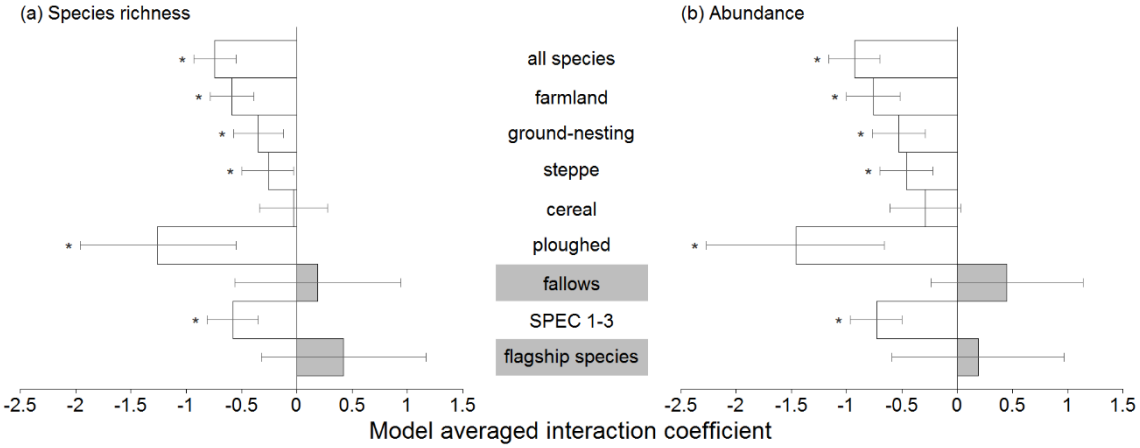

Fig. 2.4 - Estimated effects of long-term conservation investment as assessed by the interaction coefficients of models relating bird (a) species richness and (b) abundance to farmland type (SPA versus control) and sampling period (1995-97 versus 2010-12). Positive coefficients are shown as shaded bars and suggest that bird trends within the SPA were more favorable (i.e., increased more or declined less) than in the control area. Negative coefficients are shown as open bars and suggest the opposite effect. Error bars represent 95% confidence intervals. * Model probability (w_i) for each model with the interaction term (full model) ≥ 0.8.

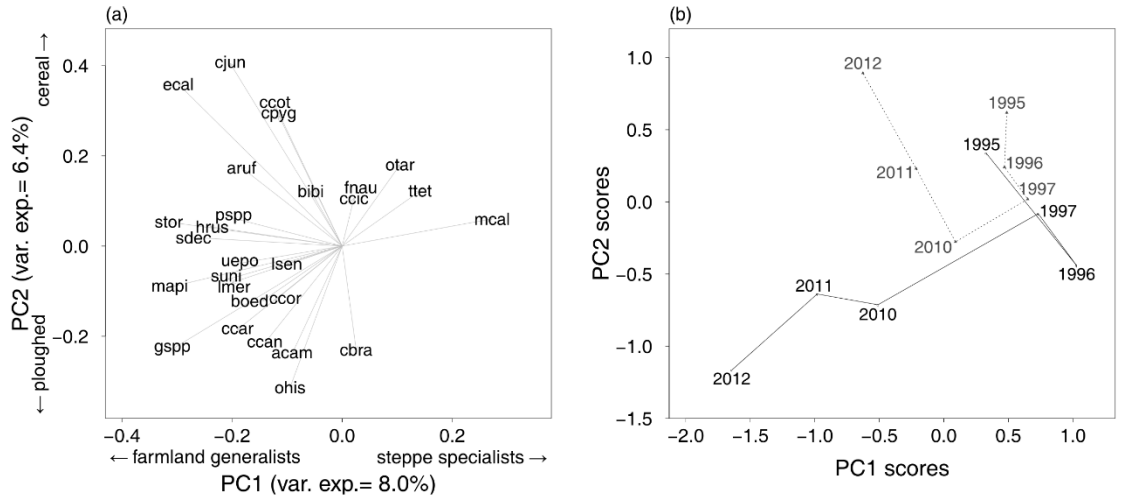

Fig. 2.5 - Biplots of a Principal Components Analysis of bird abundances in transects sampled in the Castro Verde SPA and in a control area, in 1995-97 and 2010-12: a) projection of the species, showing the gradient from steppe specialists to farmland generalists (PC1), and from ploughed to cereal field specialists (PC2); b) projection of annual mean site scores, reflecting the dominant trends of assemblage variation in the SPA (dotted lines) and the control area (full lines). Species abbreviations are provided in Table S2.4.

Variation in bird counting skills is unlikely to have affected the patterns observed, because bird detectability in open farmland is high, observers were experienced, and most observers counted birds in both the SPA and the control (98.2% of transects, Table S2.3). Selection of two areas as similar as possible (Table S2.2) should have minimized

the problem of initial landscape characteristics driving differences in bird trends (Concepción *et al.* 2012). In fact, bird assemblages observed at study outset were similar, diverging only afterwards, probably due to processes occurring during the study and not as much due to differences in initial landscape conditions. Results might also reflect unusual idiosyncrasies of the study areas, such as poor SPA management, or the emergence of conservation-oriented farming in the control. This is also unlikely, because the SPA was comparable to other Iberian cereal steppes and the most threatened species showed largely favorable trends (Pinto *et al.* 2005; Catry *et al.* 2009; Moreira *et al.* 2012; this study), while the control was a typical irrigated area undergoing agricultural intensification (Stoate *et al.* 2000). Also, building of a highway in the middle of the study period might have influenced bird trends (López-Jamar *et al.* 2011), but this is unlikely because it affected both the SPA and the control, and there were no measurable effects on very sensitive species such as the great bustard. Finally, it is conceivable that sometime during the study period bird species richness and abundance reached saturation in the SPA, causing spillover to the nearby control area. Discarding this possibility would require longer time series and detailed population data, but it is worth noting that spillover would imply increasing assemblage homogenization, whereas we observed divergence over time.

Although general biodiversity measures are often used to evaluate conservation investments (e.g., Batáry *et al.* 2001; Concepción *et al.* 2012), it is possible that metrics such as overall, farmland, and even SPEC species richness and abundance are misleading indicators of conservation success in Iberian cereal steppes. Here, these metrics may increase due to shrub encroachment, afforestation, and expansion of perennial crops (Diaz *et al.* 1998; Reino *et al.* 2009, 2010; Santana *et al.* 2012), but these processes are detrimental for the relatively species-poor but highly specialized assemblage of steppe birds that include several species of high conservation concern (Suárez *et al.* 1997; Delgado & Moreira 2000; Concepción & Díaz 2010; Reino *et al.* 2010). This probably helps to explain the most favorable trends observed in the control area, where the progressive introduction of olive groves in a landscape dominated by pastures and annual crops is likely to have increased habitat heterogeneity, and thus enhanced conditions for a wider range of generalist species (Benton *et al.* 2003). These results reinforce the point that in some cases low-intensity farmland supports poorer but more specialized bird assemblages than intensive farmland (Doxa *et al.* 2010), suggesting that evaluations of conservation investment should consider indicators reflecting assemblage specialization (Filippi-Codaccioni *et al.* 2010). Overall biodiversity measures may remain useful, however, where maintaining landscape heterogeneity and high species richness are important conservation goals (e.g., Tryjanowski *et al.* 2011).

The less favorable trends observed in the SPA for the specialized ground-nesting and steppe bird species may indicate limited conservation success, probably reflecting recent land use changes. Although AES were designed to favor the traditional farming system, the CAP reform of 2003 provided economic incentives promoting a shift to specialized livestock production (Ribeiro *et al.* 2014). There was thus a progressive increase of pasture land, at the expenses of cereal and ploughed fields, which was far more marked in the SPA than in the control (Table S2.2). The expansion of pastures should have benefited species typically associated with fallows, because the two habitats may be structurally similar (Suárez *et al.* 1997; Delgado & Moreira 2000). No effects were found for species associated to cereal fields, because declines in this habitat were similar in the SPA and the control (Table S2.2). In contrast, species associated to ploughed fields declined in the SPA due to reductions in cereal cultivation, but they increased in the control because recently planted olive groves have bare ground akin to ploughed fields. Results suggest that a mosaic of arable crops and pastures may be critical to maintain conditions for steppe birds with contrasting habitat requirements, further supporting the importance of landscape scale factors to promote conservation on farmland (Concepción & Diaz 2010; Concepción *et al.* 2012). Conservation investment appeared unable to preserve such mosaics, probably because livestock specialization driven by CAP was not counterbalanced by adequate regulations or funding schemes.

Conservation investment appeared positive on populations of highly threatened flagship species (*O. tarda*, *T. tetrax*, and *F. naumanni*), supporting the view that targeted efforts combining legal regulations and adequate funding schemes may deliver major conservation benefits (Batáry *et al.* 2011; Bretagnolle *et al.* 2011; Baker et al. 2012). Although the effects observed were relatively weak, this was probably a consequence of the generalist sampling design used in here, as other, more directed studies have demonstrated stronger positive effects (Pinto et al. 2005; Catry et al. 2009; Moreira et al. 2012). Positive trends were probably a consequence of targeted LIFE, including the purchase and management of critical areas, and the improvement of breeding and foraging habitats (Pinto *et al.* 2005; Catry *et al.* 2009; Moreira *et al.* 2012). Simultaneously, there were likely benefits from legal regulations preventing afforestation, the conversion to perennial crops, and the expansion of irrigated agriculture, which have caused detrimental changes in landscape composition and structure outside the SPA. This issue may be key, but has not been evaluated properly. The direct effect of AES is uncertain, because they apparently failed to promote the traditional rotational farming system (Ribeiro *et al.* 2014), though they may have contributed to prevent land abandonment (Stoate et al. 2009). The contrasting effectiveness observed for flagship species and other steppe birds suggests that investment concentrating on charismatic

species does not necessarily lead to the conservation of the overall steppe bird assemblage (Caro 2010).

2.6 Conclusions

Our study has some general implications for the design and evaluation of conservation investment on farmland, both in Europe and elsewhere (Attwood *et al.* 2009; Kleijn *et al.* 2011). First, we suggest that general biodiversity measures may be in some circumstances misleading indicators of conservation success. Parameters specifically tailored to reflect the outcome of conservation interventions may thus be needed, focusing for instance on the richness and abundance of groups of species of conservation concern that are specialized in specific habitat types. Second, voluntary schemes such as AES may fail to deliver its expected benefits if they are countered by more attractive economic incentives, thus calling for a better integration of conservation and agricultural policies. Third, focusing investment on flagship species may help the recovery of highly threatened species without wider benefits on less charismatic species of conservation concern, suggesting that more encompassing efforts should be developed. Finally, long-term evaluations of conservation investment are required, in order to monitor and improve the effectiveness of billions of euros needed annually for managing N2000 (Gantolier *et al.* 2010).

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2.9 Supporting Information

Table S2.1 - Summary of key conservation investments made in the Castro Verde Special Protection Area (southern Portugal) between 1993 and 2012.

Conservation Investment	Time period
Natura 2000 network	
Designation of the Castro Verde SPA under the Birds Directive (79/409/EEC) (79,066 ha; Decree-Law no. 384-B/99).	1999
Enlargement of the Castro Verde SPA (85,345 ha; Decree-Law no. 59/2008).	2008
LIFE-Nature programmes	
LIFE92 NAT/P/013900 “First phase of the conservation of steppic birds in Castro Verde” (http://ec.europa.eu/environment/life/project/Projects/index.cfm?fuseaction=search.dspPage&n_proj_id=207).	1993-1994
LIFE95 NAT/P/000178 – “Second phase of the project for the conservation of steppe birds in Castro Verde” (http://ec.europa.eu/environment/life/project/Projects/index.cfm?fuseaction=search.dspPage&n_proj_id=407).	1996-1998
LIFE02 NAT/P/008476 “Tetrax - Project Tetrax - the conservation of Little Bustard in Alentejo” (http://ec.europa.eu/environment/life/project/Projects/index.cfm?fuseaction=search.dspPage&n_proj_id=1950).	2002-2006
LIFE02 NAT/P/008481 “Peneireiro - Re-establishment of the Lesser Kestrel *Falco naumanni* in Portugal” (http://ec.europa.eu/environment/life/project/Projects/index.cfm?fuseaction=search.dspPage&n_proj_id=1953).	2002-2006
LIFE07/NAT/P/000654 “Conservation of Great Bustard, Little Bustard and Lesser Kestrel in the Baixo Alentejo cereal steppes” (http://ec.europa.eu/environment/life/project/Projects/index.cfm?fuseaction=search.dspPage&n_proj_id=3356)	2009-2012
Agri-environment schemes	
Castro Verde Zonal Plan (60,000 ha)	1995-2006
Castro Verde Integrated Territorial Intervention (ITI) (85,345 ha)	2007-2013
Research projects[(a)]	
PAMAF-8151 “Biodiversity indexes to Cork and Holm oaks”.	1998-2001
PRAXIS/P/AGR/11062/1998 "Evaluation of the effect of the hunting regime on terrestrial vertebrates"	1999-2001
Praxis XXI/C/AGR/11063/1998 “Determinants of biodiversity in fallows of pseudosteppes: implications for the definition of agri-environmental management rules”.	1999-2001
PTDC/AGR-AAM/102300/2008 “AGRIENV - Effects of agri-environment schemes on biodiversity: evaluation of a long-term landscape experiment in southern Portugal”.	2010-2013

[(a)] This list is not an exhaustive, highlighting just some of the projects with most direct implications of the conservation management of the Castro Verde SPA.

Table S2.2 - Summary of the land-use changes during the study, using the Portuguese Agricultural Census from 1999 (1995-97) and 2009 (2010-2012) for the main municipalities of the study area (see Figure 2.1): Castro Verde (SPA) and Ferreira do Alentejo (Control) (INE 1999, 2009; http://ra09.ine.pt/xportal/xmain?xpid=RA2009&xpgid=ine_ra_publicacoes&xlang=en).

Land-use	Units	SPA		Control	
		1995-1997	2010-2012	1995-1997	2010-2012
Utilized agricultural area (UAA)	ha	47,710	50,737	48,587	54,082
Mean farm size	ha	191.61	166.35	68.15	81.45
Irrigable land	% of UAA	1.18	1.60	23.06	29.46
Agricultural land	% of UAA	86.51	68.17	73.36	50.53
Annual crops	% of UAA	32.08	28.36	53.95	33.94
Cereals for grain	% of UAA	26.91	18.69	32.11	15.15
Dried leguminous	% of UAA	1.30	0.30	0.98	1.34
Temporary meadows	% of UAA	1.19	0.17	0.06	0.41
Forage crops	% of UAA	1.32	8.82	4.77	8.20
Sugar beet	% of UAA	0	0	0.91	0
Industrial crops	% of UAA	1.35	0.37	13.05	7.33
Horticultural crops	% of UAA	0.00	0.01	2.03	1.48
Flowers and ornamental plants	% of UAA	0	0	0	0.04
Fallow land	% of UAA	54.42	39.81	19.41	16.59
Perennial crops	% of UAA	1.66	2.52	6.48	21.31
Fleshy fruits	% of UAA	0.00	0.04	0.14	0.39
Citrus	% of UAA	0.04	0.01	0.02	0.34
Dry fruits	% of UAA	0	0.20	0.12	1.73
Olive	% of UAA	1.15	2.27	5.43	18.21
Vine	% of UAA	0.47	0.01	0.76	0.63
Permanent pastures	% of UAA	11.83	29.3	20.14	28.1
Vegetable gardens	% of UAA	0.01	0.05	0.01	0.03
Livestock					
Sheep	no. per UAA	0.85	0.64	0.74	0.41
Cattle	no. per UAA	0.15	0.21	0.13	0.18
Pigs	no. per UAA	0.07	0.05	0.13	0.26
Goats	no. per UAA	0.02	0.02	0.01	0.01
Horses	no. per UAA	0.00	0.00	0.00	0.01

Table S2.3 - Distribution of bird sampling effort (number of transects) and observers across farming type (SPA and Control) and period (1995-97 and 2010-12).

Year	**SPA**[a]	**Control**[a]
Total 1st Period	**46**	**32**
1995	45 (CS)	32 (CS)
1996	46 (CS)	29 (CS)
1997	39 (CS)	31 (CS)
Total 2nd Period	**46**	**32**
2010	37 (AV)	28 (AV)
2011	46 (AV,LR,SS)	32 (AV, SS)
2012	46 (AV,RM,SS)	31 (AV,RM,SS)
Total	**259**	**183**

[a] Observers: AV – Alexandre Vaz, CS – Chris Stoate, LR – Luís Reino, RM – Rui Morgado, SS – Stefan Schindler.

Table S2.4 - Mean count per transect ± standard error (minimal and maximum) and percentage of occurrence (Occ) of birds recorded in 78 plots in the Castro Verde Special Protection Area (SPA) and in a control area (Control) (southern Portugal). Species are categorized in terms of habitat specialization (Habitat) and conservation status (SPEC). For each species we indicate the conservation status in Europe (SPEC). Abbreviation (Abbr) is provided for species used in the Principal Components Analysis shown in Figure 2.5. Flagship species are underlined.

Species[1]	**Abbr**	**Habitat**[2]	**SPEC**[3]	**SPA**				**Control**				**Total** (n=442)	
				1995-97 (n=130)		2010-12 (n=129)		1995-97 (n=92)		2010-12 (n=91)			
				Mean±SE (Min-Max)	Occ (%)	Mean±SE (Min-Max)	Occ (%)	Mean±SE (Min-Max)	Occ (%)	Mean±SE (Min-Max)	Occ (%)	Mean±SE (Min-Max)	Occ (%)
Galliformes													
Alectoris rufa	aruf	Farm GN;	2	0.3±0.1(0-9)	10.8	0.4±0.1(0-4)	24.8	0.0±0.0(0-1)	3.3	0.3±0.1(0-2)	24.2	0.2±0.0(0-9)	16.1
Coturnix coturnix	ccot	Farm;GN;Step;Cere	3	0.3±0.1(0-4)	20.8	0.3±0.1(0-3)	22.5	0.4±0.1(0-4)	29.3	0.4±0.1(0-2)	33.0	0.3±0.0(0-4)	25.6
Ciconiiformes													
Bubulcus ibis	bibi	Farm	Non	0.9±0.4(0-39)	10.0	0.4±0.2(0-12)	6.2	0.1±0.1(0-5)	2.2	0.1±0.1(0-10)	1.1	0.4±0.1(0-39)	5.4
Ciconia nigra		-	2	0.0±0.0(0-1)	0.8	0	0	0	0	0	0	0.0±0.0(0-1)	0.2
Ciconia ciconia	ccic	Farm	2	0.4±0.2(0-15)	10.0	0.5±0.2(0-20)	20.9	0	0	0.1±0.0(0-2)	4.4	0.3±0.1(0-20)	10.0
Accipitriformes									0				
Elanus caeruleus		Farm	3	0.0±0.0(0-1)	0.8	0.0±0.0(0-1)	2.3	0	0	0.1±0.0(0-1)	5.5	0.0±0.0(0-1)	2.0
Milvus migrans		Farm	3	0.0±0.0(0-1)	2.3	0.0±0.0(0-1)	3.1	0	0	0.0±0.0(0-1)	3.3	0.0±0.0(0-1)	2.3
Milvus milvus		Farm	2	0	0	0.0±0.0(0-1)	0.8	0	0	0.0±0.0(0-1)	1.1	0.0±0.0(0-1)	0.5
Gyps fulvus		Farm	Non	0	0	0.1±0.1(0-14)	0.8	0	0	0	0	0.0±0.0(0-14)	0.2
Circaetus gallicus		-	3	0	0	0.0±0.0(0-1)	1.6	0	0	0.0±0.0(0-1)	1.1	0.0±0.0(0-1)	0.7
Circus aeruginosus		-	Non	0	0	0.0±0.0(0-2)	0.8	0	0	0.0±0.0(0-2)	1.1	0.0±0.0(0-2)	0.5
Circus pygargus	cpyg	Farm;GN;Step;Cere	Non	0.2±0.1(0-4)	14.6	0.2±0.0(0-2)	20.2	0.0±0.0(0-2)	2.2	0.1±0.0(0-2)	6.6	0.2±0.0(0-4)	12.0
Buteo buteo		Farm	Non	0.0±0.0(0-1)	0.8	0.0±0.0(0-2)	3.9	0.0±0.0(0-2)	1.1	0.1±0.0(0-2)	5.5	0.0±0.0(0-2)	2.7
Aquila adalberti		-	1	0	0	0.0±0.0(0-1)	2.3	0	0	0	0	0.0±0.0(0-1)	0.7
Aquila pennata		-	3	0	0	0	0	0	0	0.0±0.0(0-1)	1.1	0.0±0.0(0-1)	0.2
Aquila fasciata		Farm	3	0	0	0.0±0.0(0-1)	1.6	0	0	0	0	0.0±0.0(0-1)	0.5
Falconiformes													
Falco naumanni	fnau	Farm;Step	1	0.0±0.0(0-1)	0.8	0.6±0.2(0-16)	24.8	0	0	0	0	0.2±0.0(0-16)	7.5
Falco tinnunculus		Farm	3	0.0±0.0(0-1)	0.8	0.0±0.0(0-2)	2.3	0	0	0.1±0.0(0-3)	6.6	0.0±0.0(0-3)	2.3

Species[1]	Abbr	Habitat[2]	SPEC[3]	SPA				Control				Total (n=442)	
				1995-97 (n=130)		2010-12 (n=129)		1995-97 (n=92)		2010-12 (n=91)			
				Mean±SE (Min-Max)	Occ (%)	Mean±SE (Min-Max)	Occ (%)	Mean±SE (Min-Max)	Occ (%)	Mean±SE (Min-Max)	Occ (%)	Mean±SE (Min-Max)	Occ (%)
Gruiformes													
Tetrax tetrax	ttet	Farm;GN;Step;Fall	1	1.3±0.3(0-36)	41.5	1.2±0.1(0-10)	55.8	0.4±0.2(0-14)	16.3	0.2±0.1(0-4)	16.5	0.9±0.1(0-36)	35.3
Otis tarda	otar	Farm;GN;Step	1	0.6±0.2(0-20)	12.3	1.1±0.4(0-45)	20.9	0.0±0.0(0-0)	0	0.2±0.2(0-16)	3.3	0.5±0.1(0-45)	10.4
Charadriiformes													
Burhinus oedicnemus	boed	Farm;GN;Step;Plou	3	0.0±0.0(0-2)	3.1	0.1±0.0(0-2)	9.3	0.0±0.0(0-1)	2.2	0.2±0.1(0-2)	13.2	0.1±0.0(0-2)	6.8
Glareola pratincola		Farm;GN;Step	3	0	0	0.0±0.0(0-3)	1.6	0	0	0	0	0.0±0.0(0-3)	0.5
Pteroclidiformes													
Pterocles orientalis		Farm;GN;Step;Plou	2	0	0	0.2±0.1(0-8)	10.1	0	0	0	0	0.1±0.0(0-8)	2.9
Columbiformes													
Columba livia		Farm	Non	0	0	0.0±0.0(0-6)	0.8	0	0	0.0±0.0(0-3)	1.1	0.0±0.0(0-6)	0.5
Columba palumbus		-	Non	0	0	0.1±0.0(0-3)	6.2	0	0	0.1±0.0(0-2)	8.8	0.1±0.0(0-3)	3.6
Streptopelia decaocto	sdec	Farm	Non	0	0	0.1±0.0(0-2)	7.8	0	0	0.2±0.1(0-4)	14.3	0.1±0.0(0-4)	5.2
Streptopelia turtur		Farm	3	0	0	0.0±0.0(0-1)	0.8	0	0	0.0±0.0(0-1)	1.1	0.0±0.0(0-1)	0.5
Cuculiformes													
Clamator glandarius		Farm	Non	0.0±0.0(0-1)	0.8	0.0±0.0(0-1)	4.7	0	0	0.0±0.0(0-2)	2.2	0.0±0.0(0-2)	2.0
Cuculus canorus		Farm	Non	0.0±0.0(0-2)	3.8	0.0±0.0(0-1)	4.7	0	0	0.0±0.0(0-1)	1.1	0.0±0.0(0-2)	2.7
Strigiformes													
Athene noctua		Farm	3	0.0±0.0(0-1)	2.3	0.0±0.0(0-1)	3.9	0.0±0.0(0-1)	1.1	0.0±0.0(0-1)	3.3	0.0±0.0(0-1)	2.7
Coraciiformes													
Merops apiaster	mapi	Farm;GN	3	0.1±0.0(0-4)	8.5	0.5±0.1(0-7)	27.1	0.1±0.0(0-3)	4.3	0.4±0.1(0-3)	23.1	0.3±0.0(0-7)	16.1
Coracias garrulus		Farm;Step	2	0	0	0.0±0.0(0-1)	1.6	0	0	0.0±0.0(0-1)	1.1	0.0±0.0(0-1)	0.7
Upupa epops	uepo	Farm	3	0.2±0.0(0-4)	16.9	0.1±0.0(0-3)	10.9	0.1±0.0(0-2)	5.4	0.2±0.0(0-2)	12.1	0.2±0.0(0-4)	11.8
Piciformes													
Dendrocopos major		-	Non	0	0	0.0±0.0(0-1)	0.8	0	0	0	0	0.0±0.0(0-1)	0.2

Species[1]	Abbr	Habitat[2]	SPEC[3]	SPA				Control				Total (n=442)	
				1995-97 (n=130)		2010-12 (n=129)		1995-97 (n=92)		2010-12 (n=91)			
				Mean±SE (Min-Max)	Occ (%)	Mean±SE (Min-Max)	Occ (%)	Mean±SE (Min-Max)	Occ (%)	Mean±SE (Min-Max)	Occ (%)	Mean±SE (Min-Max)	Occ (%)
Passeriformes													
Melanocorypha calandra	mcal	Farm;GN;Step;Fall	3	1.2±0.2(0-8)	40.0	1.4±0.2(0-13)	50.4	0	0	0.0±0.0(0-1)	1.1	0.8±0.1(0-13)	26.7
Calandrella brachydactyla	cbra	Farm;GN;Step;Plou	3	0.3±0.1(0-4)	23.1	0.2±0.1(0-4)	14.7	0.1±0.0(0-1)	5.4	0.5±0.1(0-9)	28.6	0.3±0.0(0-9)	18.1
Galerida spp. *	gspp	Farm;GN;Step	3	0.2±0.0(0-3)	12.3	0.7±0.1(0-5)	48.8	0.1±0.0(0-2)	4.3	0.9±0.1(0-3)	68.1	0.5±0.0(0-5)	32.8
Lullula arborea		-	2	0.2±0.1(0-6)	10.8	0.1±0.0(0-2)	4.7	0.0±0.0(0-1)	1.1	0.1±0.0(0-2)	5.5	0.1±0.0(0-6)	5.9
Hirundo rustica	hrus	Farm	3	0.2±0.0(0-3)	10	0.3±0.1(0-5)	20.2	0.1±0.0(0-3)	5.4	0.3±0.1(0-4)	20.9	0.2±0.0(0-5)	14.3
Cecropis daurica		Farm	Non	0	0	0.0±0.0(0-1)	1.6	0	0	0.0±0.0(0-2)	2.2	0.0±0.0(0-2)	0.9
Delichon urbicum		Farm	3	0	0	0.1±0.1(0-7)	3.1	0	0	0.0±0.0(0-2)	1.1	0.0±0.0(0-7)	1.1
Anthus campestris	acam	Farm;GN;Step;Plou	3	0.0±0.0(0-1)	0.8	0.1±0.0(0-2)	7.0	0.0±0.0(0-1)	2.2	0.1±0.0(0-2)	13.2	0.1±0.0(0-2)	5.4
Motacilla flava		Farm;GN	Non	0	0	0.0±0.0(0-3)	1.6	0	0	0.0±0.0(0-1)	1.1	0.0±0.0(0-3)	0.7
Motacilla alba		Farm	Non	0.0±0.0(0-1)	0.8	0	0	0	0	0.0±0.0(0-1)	1.1	0.0±0.0(0-1)	0.5
Cercotrichas galactotes		-	3	0	0	0.0±0.0(0-1)	0.8	0	0	0	0	0.0±0.0(0-1)	0.2
Luscinia megarhynchos		-	Non	0.1±0.0(0-3)	3.1	0.1±0.0(0-4)	4.7	0.0±0.0(0-1)	2.2	0.1±0.0(0-1)	9.9	0.1±0.0(0-4)	4.8
Saxicola torquatus	stor	Farm;GN	Non	0.1±0.0(0-2)	6.9	0.3±0.1(0-6)	17.1	0.2±0.1(0-3)	10.9	0.3±0.1(0-3)	24.2	0.2±0.0(0-6)	14.3
Oenanthe hispanica	ohis	Farm;GN;Step;Plou	2	0.1±0.0(0-2)	4.6	0.0±0.0(0-2)	3.9	0.1±0.0(0-2)	5.4	0.2±0.0(0-1)	19.8	0.1±0.0(0-2)	7.7
Turdus merula		-	Non	0.1±0.0(0-2)	6.9	0.1±0.0(0-2)	7.8	0	0	0.5±0.1(0-3)	35.2	0.1±0.0(0-3)	11.5
Turdus viscivorus		-	Non	0	0	0	0	0	0	0.0±0.0(0-1)	1.1	0.0±0.0(0-1)	0.2
Cettia cetti		-	Non	0	0	0	0	0.0±0.0(0-1)	3.3	0.0±0.0(0-1)	3.3	0.0±0.0(0-1)	1.4
Cisticola juncidis	cjun	Farm;GN;Step;Cere	Non	0.4±0.1(0-4)	27.7	0.9±0.1(0-4)	51.2	0.5±0.1(0-3)	41.3	0.9±0.1(0-6)	52.7	0.7±0.0(0-6)	42.5
Acrocephalus scirpaceus		-	Non	0	0	0.0±0.0(0-1)	0.8	0	0	0	0	0.0±0.0(0-1)	0.2
Acrocephalus arundinaceus		-	Non	0	0	0	0	0	0	0.1±0.0(0-3)	2.2	0.0±0.0(0-3)	0.5
Hippolais polyglotta		-	Non	0	0	0	0	0	0	0.0±0.0(0-1)	2.2	0.0±0.0(0-1)	0.5
Sylvia atricapilla		-	Non	0	0	0	0	0	0	0.0±0.0(0-1)	1.1	0.0±0.0(0-1)	0.2
Sylvia hortensis		Farm	3	0	0	0	0	0	0	0.0±0.0(0-1)	1.1	0.0±0.0(0-1)	0.2
Sylvia undata		-	2	0	0	0.0±0.0(0-1)	1.6	0	0	0	0	0.0±0.0(0-1)	0.5

Species[1]	Abbr	Habitat[2]	SPEC[3]	SPA				Control				Total (n=442)	
				1995-97 (n=130)		2010-12 (n=129)		1995-97 (n=92)		2010-12 (n=91)			
				Mean±SE (Min-Max)	Occ (%)	Mean±SE (Min-Max)	Occ (%)	Mean±SE (Min-Max)	Occ (%)	Mean±SE (Min-Max)	Occ (%)	Mean±SE (Min-Max)	Occ (%)
Sylvia cantillans		-	Non	0	0	0.0±0.0(0-1)	0.8	0	0	0.0±0.0(0-1)	1.1	0.0±0.0(0-1)	0.5
Sylvia melanocephala		-	Non	0.2±0.0(0-2)	13.1	0.1±0.0(0-2)	7	0	0	0.1±0.0(0-1)	9.9	0.1±0.0(0-2)	7.9
Phylloscopus ibericus		-	-	0	0	0	0	0	0	0.0±0.0(0-1)	1.1	0.0±0.0(0-1)	0.2
Phyloscopus collybita		-	Non	0	0	0	0	0	0	0.0±0.0(0-1)	1.1	0.0±0.0(0-1)	0.2
Aegithalos caudatus		-	Non	0.0±0.0(0-2)	0.8	0	0	0	0	0	0	0.0±0.0(0-2)	0.2
Cyanistes caeruleus		-	Non	0.1±0.0(0-2)	8.5	0.2±0.0(0-2)	10.9	0.0±0.0(0-1)	2.2	0.1±0.0(0-2)	5.5	0.1±0.0(0-2)	7.2
Parus major		-	Non	0.3±0.1(0-7)	13.8	0.1±0.0(0-2)	10.1	0.0±0.0(0-1)	1.1	0.0±0.0(0-2)	1.1	0.1±0.0(0-7)	7.5
Certhia brachydactyla		-	Non	0.0±0.0(0-1)	2.3	0.0±0.0(0-1)	3.1	0.0±0.0(0-1)	1.1	0.0±0.0(0-1)	3.3	0.0±0.0(0-1)	2.5
Oriolus oriolus		-	Non	0	0	0.0±0.0(0-1)	0.8	0	0	0	0	0.0±0.0(0-1)	0.2
Lanius meridionalis	lmer	Farm	NA	0.1±0.0(0-1)	6.2	0.1±0.0(0-2)	9.3	0.0±0.0(0-1)	3.3	0.2±0.0(0-2)	15.4	0.1±0.0(0-2)	8.4
Lanius senator	lsen	Farm	2	0.1±0.0(0-3)	9.2	0.0±0.0(0-2)	3.9	0.1±0.0(0-4)	4.3	0.0±0.0(0-1)	3.3	0.1±0.0(0-4)	5.4
Garrulus glandarius		-	Non	0	0	0.1±0.0(0-6)	2.3	0	0	0	0	0.0±0.0(0-6)	0.7
Cyanopica cyanus		-	Non	0	0	0.1±0.0(0-3)	7.0	0	0	0.5±0.2(0-10)	19.8	0.1±0.0(0-10)	6.1
Pica pica		Farm	Non	0	0	0.0±0.0(0-1)	0.8	0	0	0.2±0.1(0-4)	17.6	0.0±0.0(0-4)	3.8
Corvus monedula		Farm	Non	0	0	0.2±0.2(0-27)	2.3	0	0	0	0	0.1±0.1(0-27)	0.7
Corvus corone	ccor	Farm	Non	0	0	0.0±0.0(0-2)	3.9	0	0	0.2±0.1(0-3)	17.6	0.1±0.0(0-3)	4.8
Corvus corax		-	Non	0.0±0.0(0-2)	3.1	0.0±0.0(0-4)	2.3	0	0	0.0±0.0(0-1)	1.1	0.0±0.0(0-4)	1.8
Sturnus unicolor	suni	Farm	Non	0.2±0.1(0-8)	10.0	0.3±0.1(0-5)	17.8	0.1±0.1(0-9)	1.1	0.3±0.1(0-11)	11	0.2±0.0(0-11)	10.6
Passer *spp***	pspp	Farm	Non	0.1±0.1(0-7)	3.1	0.6±0.2(0-100)	12.4	0.2±0.1(0-10)	4.3	1.3±0.6(0-50)	19.8	0.8±0.3(0-100)	9.5
Fringila coelebs		-	Non	0.0±0.0(0-1)	1.5	0.0±0.0(0-1)	0.8	0	0	0	0	0.0±0.0(0-1)	0.7
Serinus serinus		Farm	Non	0	0	0	0	0	0	0.1±0.0(0-1)	6.6	0.0±0.0(0-1)	1.4
Chloris chloris		Farm	Non	0	0	0.0±0.0(0-1)	3.1	0.1±0.1(0-5)	3.3	0.1±0.0(0-1)	13.2	0.1±0.0(0-5)	4.3
Carduelis carduelis	ccar	Farm	Non	0.1±0.0(0-3)	3.8	0.2±0.0(0-3)	16.3	0.0±0.0(0-2)	2.2	0.8±0.1(0-7)	40.7	0.3±0.0(0-7)	14.7
Carduelis cannabina	ccan	Farm	2	0	0	0.0±0.0(0-1)	2.3	0	0	0.4±0.1(0-7)	18.7	0.1±0.0(0-7)	4.5
Estrilda astrild		-	NA	0	0	0.0±0.0(0-0)	0	0	0	0.3±0.3(0-28)	1.1	0.1±0.1(0-28)	0.2

Species[1]	Abbr	Habitat[2]	SPEC[3]	SPA				Control				Total (n=442)	
				1995-97 (n=130)		2010-12 (n=129)		1995-97 (n=92)		2010-12 (n=91)			
				Mean±SE (Min-Max)	Occ (%)	Mean±SE (Min-Max)	Occ (%)	Mean±SE (Min-Max)	Occ (%)	Mean±SE (Min-Max)	Occ (%)	Mean±SE (Min-Max)	Occ (%)
Emberiza cirlus		Farm	Non	0	0	0.0±0.0(0-0)	0	0	0	0.0±0.0(0-1)	1.1	0.0±0.0(0-1)	0.2
Emberiza calandra	ecal	Farm;GN;Step;Cere	2	2.4±0.2(0-10)	79.2	2.2±0.2(0-8)	72.9	1.2±0.1(0-6)	60.9	1.7±0.2(0-8)	68.1	1.9±0.1(0-10)	71.3

[1] Species are listed in taxonomic order following Equipa Atlas (2008).

[2] Habitat categorization: farmland (Farm; Ehrlich et al. 1994; Equipa Atlas 2008; Reino et al. 2009; EBCC 2012); ground-nesting (GN; Ehrlich et al. 1994; Reino et al. 2009). Steppe specialists (Step; Suárez et al. 1997; Reino et al. 2009); species related to cereal fields (Cere), ploughed fields (Plou) and fallows (Fall) (Delgado & Moreira 2000, Leitão et al. 2010).

[3] Conservation status (SPEC) categories follow BirdLife International (2004): 1 - Species of global conservation concern; 2 - species concentrated in Europe and with an unfavorable conservation status; 3 - species not concentrated in Europe but with an unfavorable conservation status; Non - species with favorable conservation status; NA - not evaluated.

* *Galerida* spp.: includes *Galerida theklae*, *G. cristata* and *Galerida* sp. observations.

** *Passer* spp.: includes *Passer domesticus*, *P. hispaniolensis* and *Passer* sp. observations. We have not considered *Passer* ssp. as a SPEC species because most of the identified records were from *P. hispaniolensis* (66%).

Table S2.5 - Mean richness (number of species per transect) and abundance (number of birds per transect) ± standard error (minimum and maximum) and percentage of occurrence (Occ) of bird categories from 78 plots sampled in the Castro Verde Special Protection Area (SPA) and in a control area (Control) (southern Portugal).

Bird categories	**SPA**				**Control**				**Total** (n=442)	
	1995-97 (n=130)		**2010-12** (n=129)		**1995-97** (n=92)		**2010-12** (n=91)			
	Mean±SE (Min-Max)	Occ (%)	Mean±SE (Min-Max)	Occ (%)	Mean±SE (Min-Max)	Occ (%)	Mean±SE (Min-Max)	Occ (%)	Mean±SE (Min-Max)	Occ (%)
Richness										
All species	4.6±0.2 (0-13)	99.2	7.3±0.3 (1-18)	100	2.3±0.2 (0-8)	76.1	7.7±0.3 (2-19)	100	5.6±0.2 (0-19)	94.8
Farmland	4.0±0.2 (0-10)	99.2	6.6±0.2 (1-14)	100	2.2±0.2 (0-8)	76.1	6.5±0.3 (2-14)	100	4.9±0.1 (0-14)	94.8
Ground-nesting	3.1±0.1 (0-8)	98.5	4.6±0.2 (0-10)	99.2	1.9±0.2 (0-6)	75.0	4.0±0.2 (0-8)	97.8	3.5±0.1 (0-10)	93.7
Steppe specialists	2.8±0.1 (0-8)	98.5	4.2±0.2 (1-10)	100	1.7±0.1 (0-6)	73.9	3.3±0.2 (0-7)	96.7	3.1±0.1 (0-10)	93.4
Cereal	1.4±0.1 (0-4)	83.1	1.7±0.1 (0-4)	89.9	1.3±0.1 (0-3)	71.7	1.6±0.1 (0-4)	80.2	1.5±0.1 (0-4)	82.1
Ploughed	0.3±0.0 (0-2)	27.7	0.4±0.1 (0-4)	31.0	0.2±0.0 (0-2)	10.9	0.7±0.1 (0-4)	50.5	0.4±0.0 (0-4)	29.9
Fallows	0.8±0.1 (0-2)	62.3	1.1±0.1 (0-2)	71.3	0.2±0.0 (0-1)	16.3	0.2±0.0 (0-2)	16.5	0.6±0.0 (0-2)	45.9
SPEC 1-3	3.2±0.1 (0-7)	99.2	4.8±0.2 (1-10)	100	1.5±0.2 (0-6)	67.4	4.0±0.2 (1-9)	100	3.5±0.1 (0-10)	93.0
Flagship species	0.5±0.1 (0-2)	47.7	1.0±0.1 (0-3)	65.9	0.2±0.0 (0-1)	16.3	0.2±0.0 (0-1)	19.8	0.5±0.0 (0-3)	40.7
Abundance										
All species	11.0±0.7 (0-51)		16.2±1.1 (2-110)		3.8±0.4 (0-17)		13.5±1.0 (3-75)		11.5±0.5 (0-110)	
Farmland	9.9±0.7 (0-50)		15.1±1.0 (2-104)		3.7±0.4 (0-17)		11.5±0.9 (3-74)		10.5±0.5 (0-104)	
Ground-nesting	7.6±0.5 (0-50)		9.9±0.5 (0-51)		3.0±0.3 (0-17)		6.4±0.4 (0-18)		7.1±0.3 (0-51)	
Steppe specialists	7.1±0.5 (0-50)		9.3±0.6 (1-51)		2.7±0.3 (0-17)		5.4±0.4 (0-18)		6.5±0.3 (0-51)	
Cereal	3.3±0.3 (0-12)		3.6±0.2 (0-10)		2.1±0.2 (0-10)		3.1±0.3 (0-15)		3.1±0.1 (0-15)	
Ploughed	0.4±0.1 (0-4)		0.7±0.1 (0-9)		0.2±0.1 (0-3)		1.0±0.1 (0-9)		0.6±0.1 (0-9)	
Fallows	2.6±0.4 (0-36)		2.6±0.2 (0-15)		0.4±0.2 (0-14)		0.2±0.1 (0-4)		1.6±0.1 (0-36)	
SPEC 1-3	8.1±0.5 (0-49)		10.3±0.6 (1-51)		2.5±0.3 (0-17)		6.5±0.4 (1-18)		7.2±0.3 (0-51)	
Flagship species	2.0±0.4 (0-47)		2.8±0.5 (0-47)		0.4±0.2 (0-14)		0.5±0.2 (0-16)		1.6±0.2 (0-47)	

Table S2.6 - Model averaged coefficients [95% confidence intervals] from the five candidate models (Table 2.1), using a negative binomial family and zero inflation correction ('glmmadmb' function), relating bird species richness and abundance to farmland type (SC; Castro Verde SPA versus control area), sampling period (BA; 1995-97 versus 2010-2012), and an interaction term (SC:BA). Model probabilities (w_i) for each full model are also given.

Bird categories	**Richness**					**Abundance**				
	Intercept	SC	BA	SC:BA	*wi*	Intercept	SC	BA	SC:BA	*wi*
All species	0.81	0.68	1.20	-0.74	1	1.23	1.10	1.30	-0.93	1
	[0.59, 1.03]	[0.49, 0.87]	[0.93, 1.46]	[-0.93, -0.55]		[0.93, 1.53]	[0.88, 1.33]	[0.92, 1.68]	[-1.16, -0.70]	
Farmland	0.77	0.59	1.08	-0.59	1	1.22 [a]	1.03	1.17	-0.76	1
	[0.57, 0.98]	[0.41, 0.77]	[0.83, 1.34]	[-0.78, -0.39]		[0.94, 1.5]	[0.81, 1.26]	[0.81, 1.53]	[-1.00, -0.52]	
Ground-nesting	0.62	0.49	0.74	-0.35	0.98	1.01	0.96	0.80	-0.53	1
	[0.44, 0.8]	[0.29, 0.69]	[0.52, 0.96]	[-0.57, -0.12]		[0.76, 1.27]	[0.74, 1.19]	[0.48, 1.11]	[-0.77, -0.29]	
Steppe specialists	0.54	0.48	0.62	-0.26	0.80	0.90	0.99	0.72	-0.46	1
	[0.35, 0.73]	[0.25, 0.7]	[0.38, 0.86]	[-0.5, -0.03]		[0.64, 1.16]	[0.75, 1.23]	[0.41, 1.04]	[-0.70, -0.22]	
Cereal	0.34	0.05	0.16	-0.03	0.05	0.89	0.34	0.26	-0.29	0.37
	[0.15, 0.53]	[-0.13, 0.23]	[-0.08, 0.41]	[-0.34, 0.28]		[0.56, 1.22]	[0.06, 0.62]	[-0.14, 0.67]	[-0.61, 0.03]	
Ploughed	-2.04	0.72	1.58	-1.26	0.99	-2.02	1.03	1.83	-1.46	0.98
	[-2.63, -1.45]	[0.05, 1.4]	[0.99, 2.18]	[-1.96, -0.55]		[-2.72, -1.32]	[0.27, 1.78]	[1.12, 2.53]	[-2.27, -0.66]	
Fallows	-1.98	1.69	0.20	0.19	0.23	-1.79	2.26	-0.22	0.45	0.51
	[-2.45, -1.51]	[1.21, 2.18]	[-0.26, 0.65]	[-0.56, 0.94]		[-2.45, -1.13]	[1.53, 2.99]	[-0.93, 0.49]	[-0.24, 1.14]	
SPEC 1-3	0.40	0.76	0.98	-0.58	1	0.83	1.20	0.98	-0.73	1
	[0.19, 0.60]	[0.56, 0.96]	[0.73, 1.23]	[-0.81, -0.35]		[0.54, 1.12]	[0.97, 1.42]	[0.6, 1.35]	[-0.97, -0.50]	
Flagship species	-2.02	1.37	0.41	0.42	0.39	-1.67 [a]	1.84	0.46	0.19	0.18
	[-2.53, -1.5]	[0.82, 1.91]	[-0.19, 1.01]	[-0.32, 1.17]		[-2.38, -0.95]	[1.17, 2.50]	[-0.25, 1.17]	[-0.59, 0.97]	

[a] Negative binomial models were fit without zero inflation correction due to convergence problems.

Table S2.7 - Summary results of permutations tests (10,000 permutations) comparing results obtained with focal and random groups of species. In each case we report the percentile of the interaction coefficient estimated for the focal group in relation to the frequency distribution of coefficients estimated for random groups. Large percentiles (close to 100%) indicate that the coefficient was larger (i.e. more positive or less negative) than it might be expected by chance, whereas small percentiles (close to 0%) indicate that the coefficient was smaller (i.e. more negative or less positive) than it might be expected by chance. Finally, medium percentiles (close to 50%) indicate that coefficient was not different than expected by chance. Random groups were obtained by random sampling (without replacement) of species from a larger species pool, while maintaining the same species richness of the focal group. As groups were built hierarchically (e.g., farmland species were a subset of all species, whereas ground-nesting species were a subset of farmland species), the species pool used in each random sampling respected the same hierarchy. In some cases, random sampling produced sets of species that could not be analyzed using zero inflation models with negative binomial errors (fitted using 'glmmadmb' function, Neg. binomial) due to lack of convergence, and so these sets were discarded from analysis. The impact of this option was negligible, because similar analysis with Poisson errors and without zero inflation correction (fitted using 'glmer' function, Poisson) produced basically the same results.

Focal group	Species pool	Percentiles (%)	
		Neg. binomial	Poisson
Richness			
Farmland	All species	85.1	85.7
Ground-nesting	Farmland	84.0	83.4
Steppe specialists	Farmland	90.2	90.7
Cereal	Steppe specialists	71.6	70.2
Ploughed	Steppe specialists	8.8	9.3
Fallows	Steppe specialists	78.1	77.8
SPEC 1-3	All species	76.3	77.1
Flagship species	SPEC 1-3	95.2	94.3
Abundance			
Farmland	All species	86.1	86.4
Ground-nesting	Farmland	79.4	74.8
Steppe specialists	Farmland	83.5	81.7
Cereal	Steppe specialists	63.5	65.3
Ploughed	Steppe specialists	10.5	11.9
Fallows	Steppe specialists	90.5	85.3
SPEC 1-3	All species	79.1	78.1
Flagship species	SPEC 1-3	89.0	86.6

Table S2.8 - Model averaged coefficients [95% confidence intervals] of models relating site scores along the first two axis (PC1 and PC2) extracted from a Principal Component Analysis, to farmland type (SC; Castro Verde SPA versus control area), sampling period (BA; 1995-97 versus 2010-2012), and an interaction term (SC:BA). Model probabilities (w_i) for each full model (full model) are also given (see Table 2.1).

	Intercept	**SC**	**BA**	**SC:BA**	w_i
PC1	0.62	-0.10	-1.68	0.90	1
	[0.16, 1.09]	[-0.58, 0.39]	[-2.17, -1.19]	[0.52, 1.27]	
PC2	-0.06	0.36	-0.79	0.81	0.98
	[-0.40, 0.29]	[-0.01, 0.72]	[-1.25, -0.32]	[0.34, 1.27]	

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Chapter 3

Combined effects of landscape composition and heterogeneity on farmland avian diversity

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Keywords: agriculture intensification; biodiversity conservation; bird species richness; compositional heterogeneity; configurational heterogeneity; landscape composition.

3. Combined effects of landscape composition and heterogeneity on farmland avian diversity

3.1 Abstract

1. Conserving biodiversity on farmland is an essential element of worldwide efforts for reversing the global biodiversity decline. Common approaches involve improving the natural component of the landscape by increasing the amount of natural and semi-natural habitats (e.g., hedgerows, woodlots and ponds), or improving the production component of the landscape by increasing the amount of biodiversity-friendly crops. Because these approaches may negatively impact on economic output, it was suggested that an alternative might be to enhance the diversity (compositional heterogeneity) or the spatial complexity (configurational heterogeneity) of land cover types, without necessarily changing composition.

2. Here we develop a case study to evaluate these ideas, examining whether managing landscape composition or heterogeneity, or both, would be required to achieve conservation benefits on avian diversity in open Mediterranean farmland. We surveyed birds in farmland landscapes of southern Portugal, before (1995-1997) and after (2010-2012) the European Union's Common Agricultural Policy (CAP) reform of 2003, and related spatial and temporal variation in bird species richness to variables describing the composition, and the compositional and configurational heterogeneity, of the natural and production components of the landscape.

3. We found that the composition of the production component had the strongest effects on avian diversity, with a particularly marked effect on the richness of farmland and steppe bird species. Composition of the natural component was also influential, mainly affecting the richness of woodland/shrubland species. Although there were some effects of compositional and configurational heterogeneity, these were much weaker and inconsistent than those of landscape composition.

4. *Synthesis and Applications*. Overall, we suggest that conservation efforts in our area should focus primarily on the composition of the production component, by striving to maximise the prevalence of biodiversity-friendly crops. This recommendation probably applies to other areas such as ours, where a range of species of conservation concern is strongly associated with crop habitats.

3.2 Introduction

Conserving biodiversity on farmland is essential for reversing the global biodiversity decline, but achieving this goal has been hindered by the pervasive intensification of agricultural land uses (Krebs *et al.* 1999; Donald *et al.* 2006; Sutcliffe *et al.* 2015). Changing landscape composition (i.e., the type and amount of different land cover types) by increasing land cover by natural or semi-natural habitats preserved in agricultural landscapes (e.g. hedgerows, scrublands, riparian vegetation, woodlands, and ponds) might benefit biodiversity, as they provide key habitats for plants and animals (Ricketts 2001; Wethered & Lawes 2003), and they may act as corridors or stepping stones that facilitate dispersal among more natural areas (Hinsley & Bellamy 2000; Fischer & Lindenmayer 2002). However, significantly increasing the amount of natural habitats may be difficult or even impossible in many cases, because there is growing pressure for conservation on farmland to have minimal impacts on agricultural economic output (Green *et al.* 2005; Fischer *et al.* 2008; Tscharntke *et al.* 2012).

Meeting conservation objectives without increasing the amount of natural habitats might be achieved through changes in the crops produced, because different crop types have different structural characteristics and are associated with distinct agricultural practices that may strongly influence farmland biodiversity (Stoate *et al.* 2009, Ribeiro *et al.* 2016b). In northern Europe, for instance, sowing cereals in spring rather than in autumn increases nest sites for birds (Chamberlain *et al.* 2001; Berg et al. 2015), while producing late-harvested hay rather than early-harvested silage improves foraging habitats and increases avian nesting success (Butler *et al.* 2010). Also, farmland plants, arthropods, and birds are benefited by annual crops and pastures with more heterogeneous and sparser swards (Wilson *et al.* 2005). The production on former arable land of permanent crops such as olive orchards or energy crops such as willow short rotation coppice may also increase biodiversity, by attracting shrubland and woodland species to farmland (Sage *et al.* 2006; Rey 2011). Despite these potential benefits, however, changing crop types on private land may be difficult, because this is conditional on complex farmers' decisions driven by a combination of agricultural policies, biophysical and socioeconomic constraints, and market demands (Ribeiro *et al.* 2014).

Given these difficulties, it was recently suggested that efforts should concentrate on managing landscape heterogeneity (i.e., the diversity and spatial pattern of land cover types), without necessarily changing landscape composition (Fahrig *et al.* 2011). These efforts may focus on either the natural (i.e., natural and semi-natural habitats) or the production (i.e., different arable crops, grazed lands, orchards) components, or both, aiming to increase the compositional (i.e., richness or diversity of land cover types) or

configurational heterogeneity (i.e., complexity in the spatial arrangement of land cover types, including, e.g., diversity of patch sizes and shapes, and edge density), or both (Fahrig *et al.* 2011). This strategy seems sensible, because increasing the number of cover types may increase conditions for a larger number of species with contrasting ecological requirements, thus generating higher species richness (Pickett & Siriwardena 2011; Stein *et al.* 2014). Likewise, high diversity of cover types may favour the persistence of species that use different habitats during their life cycle or throughout the year (Chamberlain *et al.* 1999; Benton *et al.* 2003). Increasing configurational heterogeneity may also be important, because it increases the length of ecotones and interspersion/juxtaposition of habitats, which are favourable for many species (Tryjanowski 1999; Fahrig *et al*. 2011). These ideas based on landscape heterogeneity may thus provide a valuable framework to improve biodiversity conservation on farmland (Batáry *et al*. 2010; Concépcion *et al.* 2012), though its practical application in real landscapes would require further information on the relative importance of landscape composition versus heterogeneity, as well as on the relative role of the different heterogeneity components.

Here we address these issues, evaluating how landscape composition and heterogeneity affect spatial and temporal variation in avian diversity in Mediterranean farmland landscapes of southern Portugal. We focused on an extensive farmland area included in a Special Protection Area created to protect steppe bird species (Fig. 3.1) of conservation concern (Santana *et al.* 2014, and references therein), and on a neighbouring farmland area dominated by intensive agricultural land uses (Ribeiro *et al.* 2014). The study covered periods before (1995-1997) and after (2010-2012) the European Union's Common Agricultural Policy (CAP) reform of 2003, thus encompassing major changes in agricultural land uses and practices (Ribeiro *et al.* 2014, 2016a,b), and in bird assemblages (Santana *et al.* 2014), in both study areas. Based on previous ecological studies on the bird species of this region (e.g., Delgado & Moreira 2000, 2002; Reino *et al.* 2009, 2010), we tested the following expectations: (1) landscape composition of the natural component should be a strong driver of spatial and temporal variation in bird diversity, with a particularly strong positive effect of the amount of natural habitats on woodland and shrubland species; (2) landscape composition of the production component should also be influential, particularly for farmland and steppe bird species; (3) landscape compositional and configurational heterogeneity should add significantly to landscape composition in influencing bird diversity; and (4) landscape heterogeneity of the natural component should be most influential on woodland and shrubland species, while effects of the production component should be stronger on farmland and steppe birds. Results of our study were used to discuss the importance of

considering landscape composition and heterogeneity of both the production and natural components when managing farmland landscapes for conservation, and how this importance may vary widely in relation to conservation objectives.

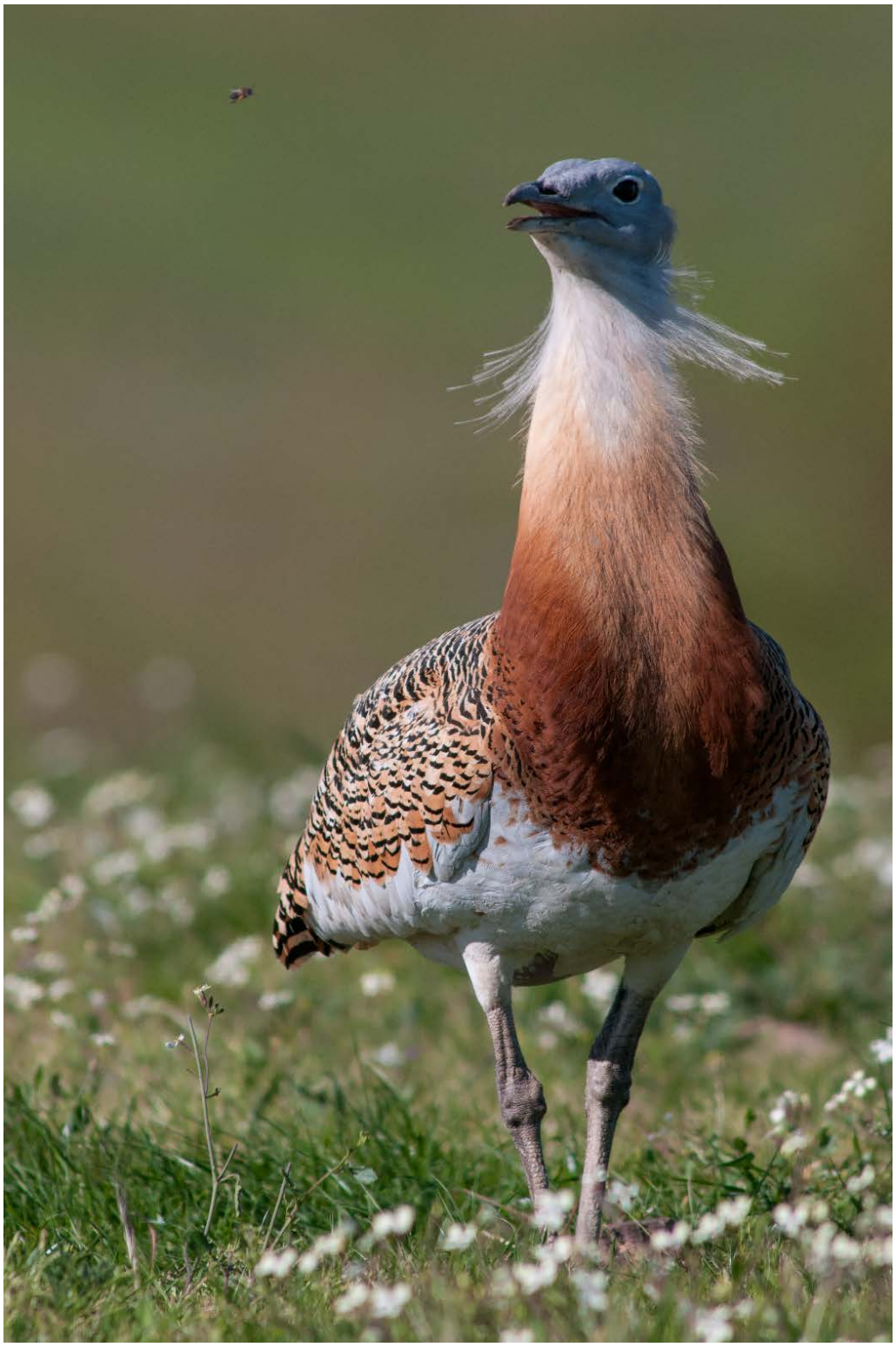

Fig. 3.1 - Great bustard (*Otis tarda*) breeding male in a grassland area within the Special Protection Area of Vila Fernando, Elvas, southern Portugal. Photograph by Luís Venâncio.

3.3 Materials and Methods

3.3.1 Study area

The study was conducted in a Mediterranean agricultural region of southern Portugal (Fig. 3.2), within a low-intensity farmland area included in the Special Protection Area (SPA) of Castro Verde (37º 41´ N, 8º 00´ W), and within the nearby (about 10 km) high-intensity farmland area of Ferreira do Alentejo (38º 03´ N, 8º 06´ W). Before the CAP reform of 2003, agriculture in the low-intensity area was dominated by the traditional rotation of rain-fed cereals and fallows typically grazed by sheep, which provides habitat for a range of steppe bird species (Delgado & Moreira 2000; Santana *et al.* 2014). Following the CAP reform there were marked shifts from the traditional system towards the specialized production of either cattle or sheep, with declines in cereal and fallow land, and increases in permanent pastures (Ribeiro *et al.* 2014). Throughout the study period, this area benefited from significant conservation efforts, including agri-environment schemes, legal restrictions to afforestation and land use intensification, and projects targeting steppe birds (Ribeiro *et al.* 2014; Santana *et al.* 2014). In contrast to Castro Verde, the high-intensity area had irrigation infrastructures, better soils, and no constraints to crop conversion (Ribeiro *et al.* 2014). Before the CAP reform, agriculture in this area was dominated by intensive, annual irrigated crops, but thereafter there was a progressive shift to permanent crops (mainly olive groves) (Ribeiro *et al.* 2014).

3.3.2 Study design

The study was based on the modelling of spatial and temporal variation in the species richness of breeding bird assemblages in relation to variables describing landscape composition and heterogeneity. Spatial variation was analysed on two occasions, corresponding to periods before (1995–1997) and after (2010-2012) the CAP reform of 2003. Temporal variation was estimated from differences in richness between the two time periods. Sampling was based on a network of 250-m transects set in 1995, which were initially designed to evaluate the effects of an agri-environment scheme, with 46 transects set in the SPA of Castro Verde and 32 in the nearby area of Ferreira do Alentejo (Stoate *et al.* 2000; Santana *et al.* 2014). Transects followed a random bearing, and they started at grid intersections of a 1-km square grid overlaid on the study area, which were selected based on access constraints and the presence of agricultural land uses (Stoate *et al.* 2000). From the initial pool of 78 transects, we retained 73 that were surveyed in at least two years in each of the two time periods (mean counts per transect ± SD; min-

max = 5.8±0.4; 5-6). Landscape variables were estimated within 250-m buffers (32.12 ha) of each transect (Fig. 3.2).

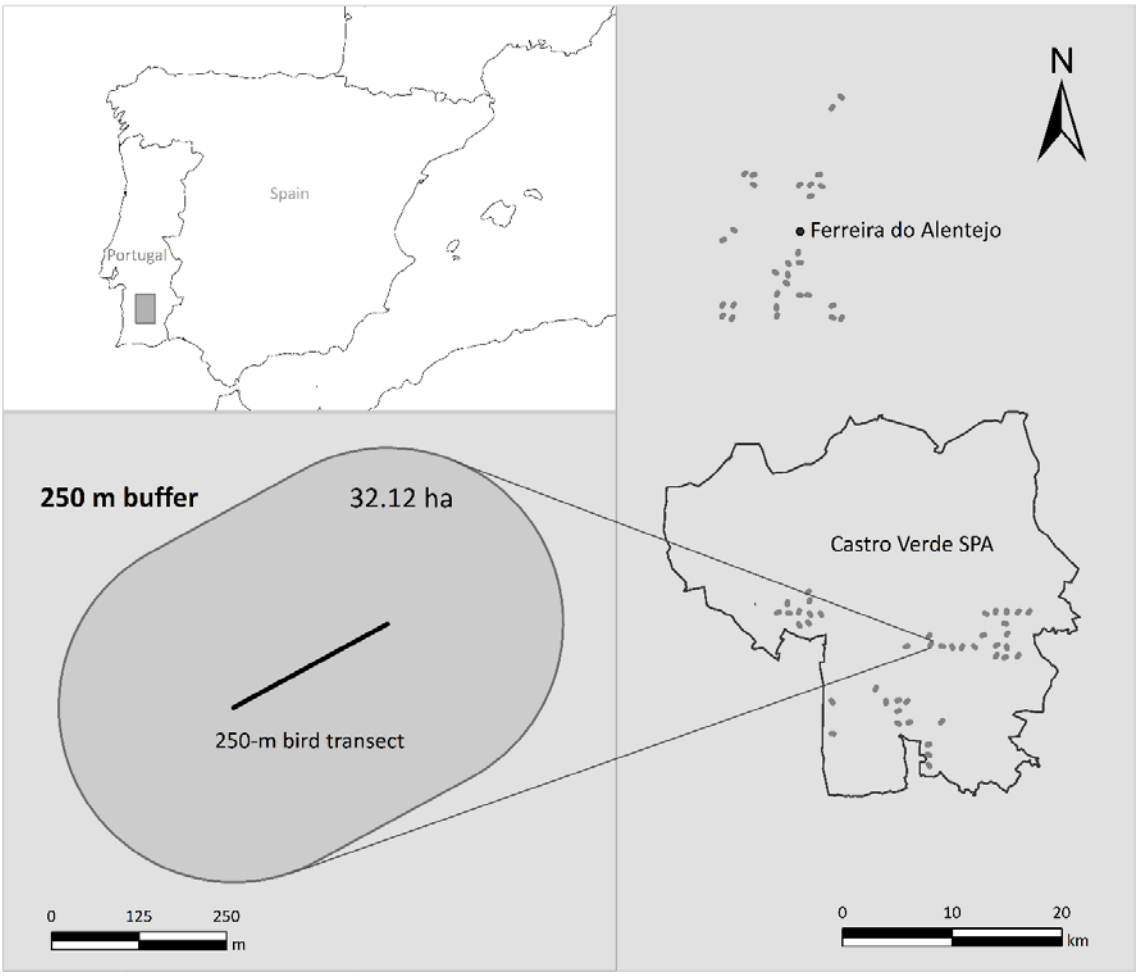

Fig. 3.2 - The study area in southern Portugal, showing its location in the Iberian Peninsula (upper left panel), the distribution of 73, 250-m bird sampling transects in relation to the Special Protection Area (SPA) of Castro Verde (right panel), and an example of a 250-m buffer around a transect where landscape composition and heterogeneity were characterized (lower left panel).

3.3.3 Bird surveys

Birds were sampled three times per time period in each transect, corresponding to one sampling occasion per year and transect in 1995-1997 and 2010-2012. Sampling was conducted during the breeding season in April-May, which was deemed adequate to maximise the chances of detecting both resident and trans-Saharan migratory species (Reino *et al.* 2009, 2010). Transects were walked in early morning and late afternoon, and all birds observed within 250 m were registered (Santana *et al.* 2014). Species richness was estimated from the total number of species registered per transect in either 1995-1997 or 2010-2012. Bird data were pooled per time period to increase species detectability and to minimise potential confounding effects resulting from year-to-year

fluctuations in species occurrences unrelated to local habitat conditions, differences in observer skills, and the possibility of missing some species when sampling on a single sampling occasion per year. To test for differential landscape effects on different species groups, we computed both the total species richness and the richness of species categorised according to major habitat affinities (Table S3.1): i) woodland birds – species dependent on woodlands and shrublands; ii) farmland birds - species associated with all farmland habitat types (e.g. arable fields, permanent crops, hedgerows); and iii) steppe birds – a subset of farmland species occurring only in open grassland habitats (Gil-Tena *et al.* 2007; Reino *et al.* 2009, 2010; Santana et al. 2014). Aquatic birds were excluded because they were inadequately sampled by our approach. See Santana *et al.* (2014) for methodological details.

3.3.4 Landscape composition and heterogeneity

For each buffer around each transect, we prepared land cover maps for 1995-1997 and 2010-2012, using digital aerial photographs from 1995 (scale 1:40,000), and Bing Aerial images from October 2010 to July 2011 (http://mvexel.dev.openstreetmap.org/bing/), respectively. The minimum mapping unit was 50-m^2, and we differentiated all land cover categories that could be readily identified in the photographs. Using a single land cover map for each 3-year period was considered reasonable because bird data were also pooled for the same periods, and because land cover categories were not expected to drastically change within each period. Mapping was refined with information from a governmental database of agricultural land uses at the parcel scale (details in Ribeiro *et al.* 2014), using data from 2000 and 2010 to represent crop types in 1995-1997 and 2010-2012, respectively. The 3 to 5 years mismatch in the first period was considered reasonable, because it corresponded to a time of relative stability in agricultural land uses before the Common Agricultural Policy (CAP) reform of 2003 (Ribeiro *et al.* 2014). Therefore no major annual variations in the production component were expected, particularly considering the broad land cover categories used (see below). Furthermore, the information on agricultural land uses was cross-checked with information from aerial photographs and the official land cover maps of Continental Portugal for 1990, further guaranteeing that no significant land use changes would be missed. Cartography for 2010-2012 was further refined using the official land cover maps of Continental Portugal for 2007.

Detailed land cover types in the preliminary map were categorized in 11 broad categories, which were defined to have management relevance (e.g., Ribeiro *et al.* 2014, 2016b) and to reflect functionally important habitats for regional bird assemblages (Fig. S3.1). Specifically, we considered categories reflecting the natural component of the

landscape (woodlands, open woodlands, shrublands, streams, and water bodies), which were expected to be particularly important for different woodland and shrubland species, and categories reflecting the production component (annual dry crops and fallows, permanent pastures, annual irrigated crops, arable land with scattered trees, and permanent crops), which were expected to be particularly important for different farmland species (e.g., Moreira 1999; Delgado & Moreira 2000; Stoate *et al.* 2000; Reino *et al.* 2009, 2010; Santana *et al.* 2014). Landscape composition was then estimated as the proportional cover by each land cover category. The same categories were used to estimate variables describing the heterogeneity of both the natural and production components of the landscape. Following Fahrig *et al.* (2011), landscape compositional heterogeneity was described from the richness, diversity and evenness of land cover categories, while landscape configurational heterogeneity was described from the largest patch index, mean patch size, edge density and mean shape complexity (details in Table S3.2). Landscape metrics were estimated in a GIS using Fragstats 4.2 (McGarigal & Ene 2013).

3.3.5 Statistical analysis

In each time period, we modelled spatial variation in species richness in relation to landscape variables using generalized linear models (GLM) with Poisson errors and log link (dispersion parameter close to 1, mean ± SD = 1.06 ± 0.38), while we used GLMs with Gaussian errors and identity link to model temporal variations in species richness. In temporal analyses, variations in species richness were measured by subtracting species richness of 1995-1997 from that of 2010-2012, while temporal variation in landscape variables was estimated likewise by subtracting the values of the first period from those of the second (e.g., Δ Edge density = Edge density [2010-2012] – Edge density [1995-1997]). Before analysis, landscape variables were transformed using the angular transformation for proportional data and the logarithmic transformation for continuous variables, thereby minimizing potential problems associated with the unit sum constraint and the undue influence of extreme values.

Model building procedures were based on the information theoretic approach with multi-model inference (Burnham & Anderson 2002). First, we estimated for each dependent variable the relative importance of landscape composition, compositional heterogeneity and configurational heterogeneity, of either the natural or the production components (Table 3.1), based on 63 a priori candidate models corresponding to all possible combinations of these six sets of variables (Table S3.3). Each set appeared in the same number of models (32), and each variable appeared in a model with every other variable. For all candidate models, we calculated model probabilities (Akaike

weights, w_i) based on Akaike information criterion corrected for small sample sizes (AICc). The importance of each set of variables was then calculated by the sum of the w_i (w_i+) of the models where each variable set was present. Second, sets of variables with $w_i+ > 0.5$ were carried over to a subsequent modelling step, where we built average models to evaluate the importance of each individual variable to explain variation in species richness. In this case, candidate models were built from all combinations of variables included in analysis.

To assess the relative importance of variables and to build average models, we used the procedure of Cade (2015), which explicitly acknowledges that the independent variables were intercorrelated to greater or lesser degrees, and that the statistical expression of the effects of one variable may change depending upon which other variables are included in any particular model (Herzog *et al.* 2006; Cushman *et al.* 2012). Therefore, we computed model averaging for the partial standardized coefficients obtained by multiplying the unstandardized coefficient in the model by the partial standard deviation of the variable, which is a function of the standard deviation of the variable in the sample, the sample size, the number of variables in the model, and the variance inflation factor of the variable (Cade 2015). Then, we estimated the relative importance of each variable within each model as the ratio of its partial standardized regression coefficient (absolute value) to the largest partial standardized regression coefficient (absolute value) in the model (Cade 2015). This approach examines the importance of each set of variables in the context of every other combination of variable sets, and the importance of each individual variable in the context of its contribution relative to other variables in a model, independently of the variable set (Cade 2015).

To evaluate spatial autocorrelation problems that might produce biased model coefficients (Diniz-Filho *et al.* 2008), we used spline correlogram plots with 95% pointwise confidence intervals calculated with 1000 bootstrap resamples (Bjørnstad & Falck 2001). We inspected correlograms for both the raw data and model residuals, to assess whether autocorrelation was effectively removed in the modelling process. We assumed that variable selection and parameter estimation was unbiased when there was no significant autocorrelation in model residuals (Diniz-Filho *et al.* 2008; Rhodes *et al.* 2009).

All analyses were performed using R 3.2.5 (R Core Team 2016). GLMs were performed using ‘glm’ function in MASS package (Venables & Ripley 2002), Akaile weights were calculated using ‘akaike.weights’ function in qpcR (Spiess 2014), model averaging was performed using ‘model.avg’ and ‘partial.sd’ functions in MuMIn (Barton 2016), spline correlograms were plotted using ‘spline.correlog’ and ‘plot.spline.correlog’ functions in ncf (Bjørnstad & Falck 2001).

Table 3.1 - Summary statistics (mean ± standard error [SE]; minimum [Min] and maximum [Max]) of variables describing landscape composition and heterogeneity in 250-m buffers around 73 transects used to estimate bird species richness in 1995-1997 and 2010-2012, in southern Portugal. Temporal variation indicates differences between the second and the first period, and significant deviations from zero ($P < 0.05$; paired t-test) are underlined. Variables are organized according to six sets *[#]* used in data analysis. Landscape composition variables are expressed in percentage cover (%) and are described in Fig. S3.1. Description and units of heterogeneity variables are given in Table S3.2.

Landscapes variables	**1995-1997**		**2010-2012**		**Temporal Variation**		**Paired t-test**	
	Mean±SE	(Min,Max)	Mean±SE	(Min,Max)	Mean±SE	(Min,Max)	t	*P*
Natural component								
[1] Composition								
Woodland	2.3±1	(0,58.2)	1.5±0.5	(0,23.5)	-0.8±0.7	(-47.4,10.3)	-0.84	0.403
Open woodland	6.7±2.1	(0,80)	7.9±2.4	(0,78.4)	1.3±1.4	(-33.4,54.6)	0.74	0.462
Shrubland	1.4±0.3	(0,12.9)	1.4±0.4	(0,20.9)	0±0.2	(-6.6,10.2)	-1.72	0.091
Streams	1.1±0.3	(0,15.2)	1.1±0.3	(0,15.2)	0±0.1	(-2.5,1.3)	-0.28	0.783
Water bodies	0.1±0.0	(0,2)	0.6±0.2	(0,16.5)	**0.5±0.2**	**(-0.1,16.5)**	**3.10**	**0.003**
[2] Compositional heterogeneity								
Land cover richness	1.5±0.1	(0,4)	1.5±0.1	(0,5)	0.1±0.1	(-1,2)	0.75	0.456
Land cover diversity	0.3±0.0	(0,1.1)	0.3±0	(0,1.3)	0±0	(-0.6,0.6)	-0.17	0.863
Land cover evenness	0.3±0.0	(0,1)	0.3±0	(0,1)	0±0	(-0.9,0.8)	-0.18	0.854
[3] Configurational heterogeneity								
Largest patch index	6.3±1.8	(0,73.7)	7.1±1.9	(0,72.8)	0.8±0.8	(-21.2,49.8)	1.07	0.289
Patch size	0.6±0.2	(0,11.1)	0.7±0.2	(0,11.2)	0.1±0.1	(-1.3,3.4)	1.03	0.304
Edge density	68.3±10.1	(0,340.9)	67.5±10.8	(0,387.3)	-0.8±3.8	(-127,88.8)	-0.08	0.933
Shape complexity	2.1±0.2	(0,7.5)	2±0.2	(0,6.9)	0±0.1	(-4,3.4)	0.29	0.770
Production component								
[4] Composition								
Arable land with scattered trees	4±1.1	(0,59.3)	2.4±1	(0,59.4)	**-1.6±0.6**	**(-34.5,1.7)**	**-3.05**	**0.003**
Annual dry crops	50.2±3.8	(0,100)	20.8±3.3	(0,99.4)	**-29.4±4.4**	**(-98.9,72.7)**	**-6.82**	**<0.001**
Permanent pastures	17.7±3.4	(0,99.6)	36.6±4.6	(0,99.4)	**18.9±3.9**	**(-51.2,99.4)**	**4.83**	**<0.001**
Annual irrigated crops	14.6±2.9	(0,95.6)	8.8±2.3	(0,87.6)	**-5.7±2.6**	**(-95.6,51.3)**	**-2.74**	**0.008**
Permanent crops	1.6±0.7	(0,47.8)	18.2±3.9	(0,100)	**16.6±3.8**	**(-8.3,100)**	**4.30**	**<0.001**
[5] Compositional heterogeneity								
Land cover richness	2.3±0.1	(1,4)	2.2±0.1	(1,4)	-0.1±0.1	(-2,1)	-1.16	0.252
Land cover diversity	0.5±0	(0,1.2)	0.4±0	(0,1.1)	**-0.1±0**	**(-0.8,0.7)**	**-2.61**	**0.011**
Land cover evenness	0.6±0	(0,1)	0.4±0	(0,1)	**-0.1±0.1**	**(-1,0.9)**	**-2.73**	**0.008**
[6] Configurational heterogeneity								
Largest patch index	61.6±3.1	(5.2,100)	63.7±3.2	(9.5,100)	2.1±2.2	(-64.5,48.1)	1.24	0.219
Patch size	10±0.9	(0.3,32.1)	10.1±0.9	(0.4,32.1)	0.1±0.9	(-23.1,22.7)	-0.02	0.980
Edge density	90±7.5	(0,346.6)	82.6±8.1	(0,366.4)	-7.4±4.6	(-151.1,144.7)	-1.50	0.138
Shape complexity	1.8±0.1	(1.2,3.6)	1.7±0	(1.1,3.1)	-0.1±0	(-1.4,0.9)	-1.46	0.148

3.4 Results

3.4.1 Overall patterns

On average, the highest species richness per transect was found for farmland and steppe birds, while there were relatively few woodland species (Fig. 3.3). The mean species richness of overall, woodland, and farmland bird assemblages doubled between 1995-1997 and 2010-2012, while the temporal increase in steppe bird species richness was small, albeit statistically significant (Fig. 3.3). Farmland and steppe birds occurred in nearly every transect in both periods, whereas the prevalence of woodland birds increased from 30% to 60%.

Landscape composition was strongly dominated by the production component, though with marked temporal changes in the relative importance of land cover categories (Table 3.1). There were strong decreases in cover by annual dry crops, arable land with scattered trees, and annual irrigated crops, and increases in permanent pastures and permanent crops. The natural component occupied a much smaller proportion of the landscape, and it was mainly represented by woodlands and open woodlands (Table 3.1). Only the cover by water bodies changed significantly (increased) over time. Landscape heterogeneity varied little over time, though there was a reduction in the compositional heterogeneity of the production component, with significant declines in land cover diversity and evenness (Table 3.1).

There was strong support for landscape effects on spatial and temporal variation in species richness, with one to three sets of landscape variables showing summed Akaike weights >0.50 in the models for different time periods and species groups (Table 3.2). Average models further confirmed strong effects of individual landscape variables (Fig. 3.4), though their explanatory power was much higher for spatial (R^2: 0.15 – 0.78) than for temporal (R^2: 0.06 – 0.25) variations (Tables S3.4 - S3.6). Spline correlograms pointed out strong spatial autocorrelation in the raw data, but that this was successfully removed by the landscape models, as there was no significant autocorrelation in the residuals (Figs. S3.2 – S3.5).

3.4.2 Effects of landscape composition

In line with expectations, the composition of the natural component contributed to explain spatial variation in total species richness in 2010-2012 ($w_i+ = 0.69$), and that of woodland birds in both periods ($w_i+ = 0.70$ and 0.96), but did not influence farmland and steppe birds (Table 3.2). Total species richness in 2010-2012 increased with increasing cover by streams (Fig. 3.4, Table S3.5). The richness of woodland birds increased along with cover by woodland and open woodland in 1995-1997, but no individual variable was

particularly important in 2010-12 (Fig. 3.4, Table S3.4,S3.5). Temporal variation in species richness was little affected by the composition of the natural component (Fig. 3.4, Table S3.6).

Also in line with our expectations, the composition of the production component was an important predictor of spatial and temporal variation in species richness (Table 3.2). The effects on spatial variation were particularly marked for total species richness (w_i+ = 1.00) and that of farmland (1.00) and steppe birds (0.99) in 1995-1997, and for species richness of woodland (0.99) and steppe birds (0.96) in 2010-2012 (Table 3.2). All production cover categories were negatively related to total species richness in 1995-1997, albeit with much stronger effects of arable land with scattered trees and annual irrigated crops (Fig. 3.4, Table S3.4). Permanent pastures and annual dry crops had negative effects on woodland birds in 2010-2012, and positive effects on steppe birds in both periods (Fig. 3.4, Table S3.4 and S3.5). Arable land with scattered trees and annual irrigated crops were negatively related to the richness of farmland birds in 1995-1997 (Fig. 3.4, Table S3.4). The composition of the production component had particularly marked effects on the temporal variation of total (w_i+ = 0.96) and woodland (1.00) bird species richness (Table 3.2). For both groups, richness was positively related with cover by permanent crops, and the total species richness also increased with declining cover by arable land with scattered trees (Fig. 3.4, Table S3.6).

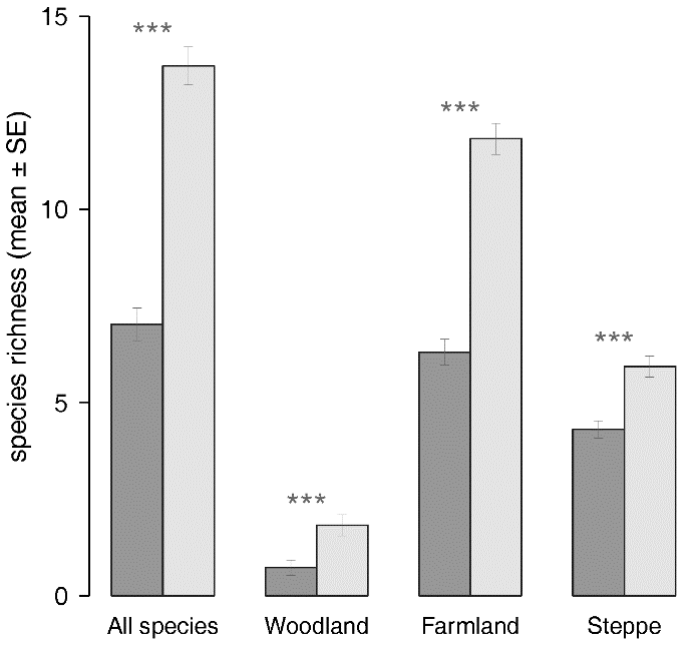

Fig. 3.3 - Mean species richness (± standard error) of bird assemblages (all species, woodland, farmland and steppe) estimated in 250-m buffers around 73 transects, in 1995-1997 (dark grey bars) and in 2010-2012 (light grey bars). Significant differences (P < 0.001; paired t-tests) between time periods are marked with ***.

Table 3.2 - Relative importance of sets of variables describing composition, compositional heterogeneity and configurational heterogeneity of either the natural or production components of the landscape, to explain spatial (T0: 1995-1997 and T1: 2010-2012) and temporal (Δt) variation in bird species richness in farmland landscapes of southern Portugal. The importance of each set of variables was estimated as the sum of Akaike weights (w_i+) of candidate models where that set occurs, considering a pool of 63 candidate models involving all combinations of sets of variables. Sets with w_i+ > 0.5 were carried over to subsequent analysis and are given in bold.

Variable set	All species			Woodland			Farmland			Steppe		
	T0	T1	Δt	T0	T1	Δt	T0	T1	Δt	T0	T1	Δt
Composition												
Natural component	0.05	**0.69**	0.02	**0.70**	**0.96**	0.00	0.02	0.12	0.03	0.01	0.02	0.01
Production component	**1.00**	0.28	**0.96**	0.02	**1.00**	**0.99**	**1.00**	0.03	0.22	**0.99**	**0.96**	0.07
Compositional heterogeneity												
Natural component	0.10	0.32	0.26	0.22	0.04	0.03	0.19	0.14	**0.65**	0.14	0.03	**0.94**
Production component	**0.76**	0.26	0.35	0.14	0.07	0.08	**0.56**	0.06	0.27	0.04	0.04	0.18
Configurational heterogeneity												
Natural component	0.06	**0.53**	0.02	0.35	**0.99**	0.05	0.13	0.25	0.04	0.05	0.06	0.04
Production component	0.12	0.12	0.01	0.25	0.00	0.03	0.07	**0.63**	0.03	0.02	0.02	0.05

3.4.3 Effects of compositional and configurational landscape heterogeneity

According to our expectations, we found some effects of both compositional and configurational heterogeneity on species richness, though these effects were generally weaker than those of landscape composition (Table 3.2). We also found some evidence that heterogeneity of the natural component had stronger effects on woodland than on farmland and steppe bird species, and the opposite for the heterogeneity of the production component, though the effects were generally weak and partly inconsistent (Table 3.2).

Regarding the natural component, the compositional heterogeneity did not influence spatial variation in species richness, but configurational heterogeneity contributed to woodland (w_i+ = 0.99) and, to a much lesser extent, total (w_i+ = 0.53) bird species richness in 2010-2012 (Table 3.2). Total species richness increased along with patch size, and declined with shape complexity (Fig. 3.4, Table S3.5), while there was a weak tendency for woodland bird richness to increase with patch size (Fig. 3.2, Table S3.9). Compositional heterogeneity contributed to temporal variations in farmland (w_i+ = 0.73) and steppe (w_i+ = 0.95) bird species richness (Table 3.2). The richness of steppe birds increased with the richness and evenness of natural cover categories, whereas the later was also positively related to farmland bird richness (Fig. 3.4, Table S3.6).

Heterogeneity of the production component had weak to no effects on spatial variation in species richness, and no effects on temporal variations (Fig. 3.4, Table S3.4 – S3.6). The compositional heterogeneity contributed moderately to variation in total species richness in 1995-1997 (w_i+ = 0.68) (Table 3.2), when it increase along with crop diversity (Fig. 3.4, Table S3.4). The configurational heterogeneity contributed moderately

to farmland bird species richness in 2010-2012 ($w_i+ = 0.64$) (Table 3.2), when there was a positive effect of edge density (Fig. 3.4, Table S3.5).

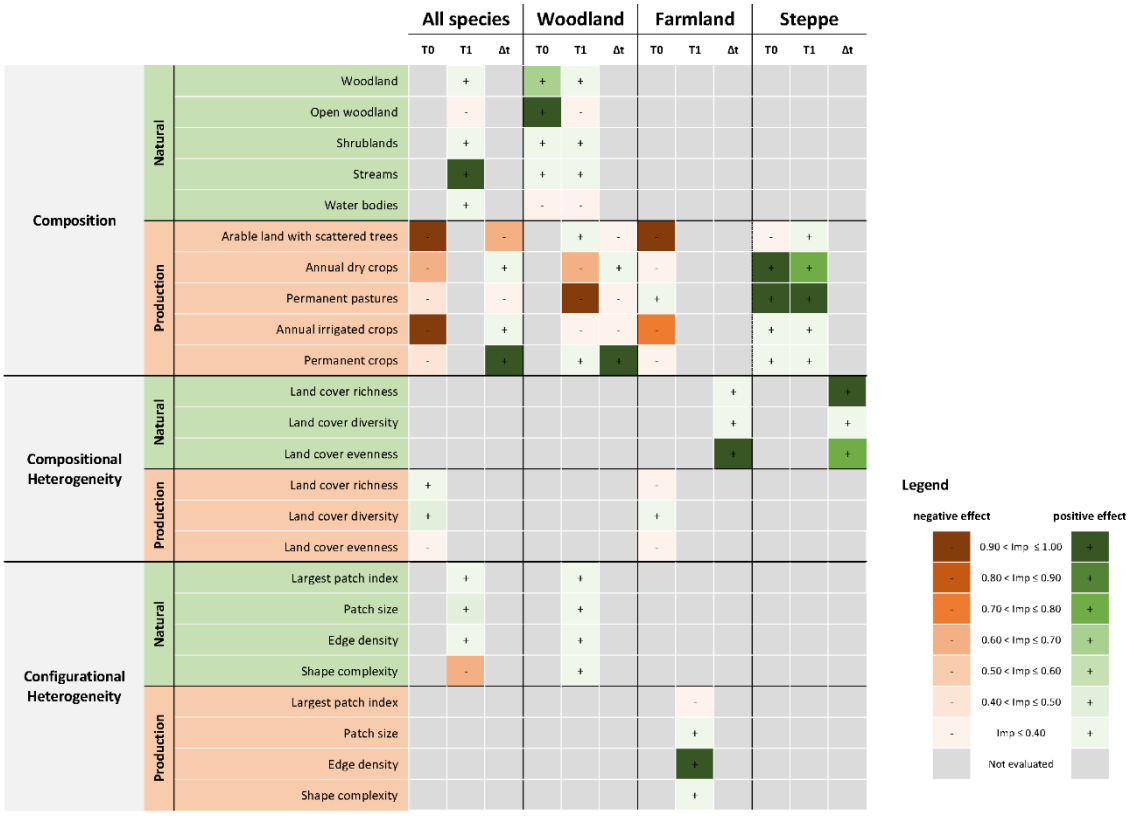

Fig. 3.4 - Graphical representation of the relative importance of landscape variables to explain spatial (T0 = 1995–1997, T1 = 2010–2012) and temporal (Δt) variation in bird species richness in farmland landscapes of southern Portugal. The importance of landscape variables was estimated from average models built separately for each of four bird assemblages (all species, woodland, farmland, and steppe). The variables used in modeling reflect composition, compositional heterogeneity, and configurational heterogeneity, of the natural and production components of the landscapes

3.5 Discussion

Our study examined the relative role of landscape composition and heterogeneity on spatial and temporal variations in avian diversity in Mediterranean farmland, showing that the composition of the natural and the production components had far stronger effects than those of their compositional or configurational heterogeneity (*sensu* Fahrig *et al*. 2011). Specifically, our study supported the expectation that the natural component should have a strong effect on species richness, in particular that of woodland and shrubland birds, while the effects of the production component should also be strong, particularly on farmland and steppe bird species. In contrast, the effects of heterogeneity were relatively weak and inconsistent, with few clear relationships between species richness and variables describing the diversity of land cover types (i.e., compositional heterogeneity) or the spatial arrangement of such cover types (i.e., configurational

heterogeneity). These results might be seen as surprising, considering the prominent role given to heterogeneity as a key driver of farmland biodiversity (Benton *et al.* 2003; Fahrig *et al*. 2011), but they are consistent with a vast literature pointing out the strong effects of crop type and management (Chamberlain *et al.* 2001; Wilson *et al.* 2005; Stoate *et al.* 2009; Butler *et al*. 2010; Rey 2011; Berg *et al.* 2015; Hiron 2015; Josefsson *et al.* 2016). Overall, therefore, our results suggest that both composition and heterogeneity should be duly considered when managing farmland landscapes for conservation, with a particular emphasis on the identity and amount of different crop types because these may have far reaching consequences on species richness.

3.5.1 The natural component of the landscape benefited avian diversity

The expectation that avian diversity is strongly shaped by the composition of the natural component of the landscape was mainly supported by the positive relation between streams and overall species richness, and between woodlands and the richness of woodland/shrubland species. Streams covered only a very small proportion of the landscape but they were important possibly because they were often associated with arboreal and shrubby riparian galleries, which tend to be occupied by a number of woodland, shrubland and specialised riparian species that are absent in surrounding open farmland (Pereira *et al.* 2014). Transects close to streams thus sampled those species, together with more typical farmland species, thereby justifying their positive influence on overall diversity. It is worth noting, however, that streams were only influential after the CAP reform of 2003, when there was a marked increase in the pool of woodland/shrubland species in the study area (Santana *et al*. 2014; this study).

In contrast to streams, woodlands favoured the richness of woodland/shrubland species but were poor predictors of overall diversity, though they are known to be species-rich habitats (Santana *et al.* 2012), and diversity tends to increase with the size of woodland patches (Santos *et al.* 2002). However, woodlands tend to be unsuitable for a range of farmland species, particularly steppe birds due to habitat loss and edge effects (Reino *et al.* 2009; Morgado *et al.* 2010; Batáry *et al.* 2011; Concepción & Díaz 2011; Fischer *et al.* 2011; Moreira *et al*. 2012), and so there was probably a trade-off between increases in woodland species and declines in some farmland species.

3.5.2 Composition of the production component was key to avian diversity

Also in line with expectations, the composition of the production component showed strong effects on species richness. Effects were generally stronger on farmland and steppe birds, probably because they often live within the production area, and so they should be particularly affected by the identity and amount of different crop types

represented in farmland landscapes (Chamberlain et al. 2001; Wilson et al. 2005; Stoate et al. 2009; Butler et al. 2010; Rey 2011; Berg et al. 2015; Hiron 2015; Josefsson et al. 2016). This is illustrated by the strong negative effects of cover by annual irrigated crops on the species richness of farmland birds observed in 1995-1997, that was probably a consequence of these crops providing poor breeding and foraging habitats for a range of species (Brotons *et al.* 2004; Stoate *et al.* 2009). The negative effects of arable land with scattered trees probably reflect the same mechanism, as this land cover type was often associated with the production of annual irrigated crops. The species richness of steppe birds was positively affected by the amount of annual dry crops and permanent pastures in both study periods, probably because most of these species are associated with these habitat types (Moreira 1999; Delgado & Moreira 2000; Stoate *et al.* 2000; Reino *et al.* 2009, 2010).

The composition of the production component also affected the overall diversity, but this was probably mediated to a considerable extent by the effects on farmland birds, which are the dominant group in the region. For instance, the negative relationship observed between total species richness and cover by arable land with scattered trees and by annual irrigated crops was probably a consequence of the strongly negative effect of these habitats on farmland birds. However, the production component also affected non-farmland birds, which was clearly underlined by the positive effects of permanent crops on the spatial (in 2010-2012) and temporal increase in woodland bird species richness. Permanent crops in our area were mainly olive orchards, which have structural similarities with woodlands, and may thus attract species that otherwise would be rare or absent in open arable farmland (Rey 2011). As a consequence, cover by permanent crops showed strongly positive effects on total species richness, although these habitats are known to be avoided by a range of steppe birds associated with open farmland habitats (Stoate *et al.* 2009).

Despite the strong effects of the production component, the influential crops varied between study periods, which was probably a consequence of the major changes in agricultural land uses associated with the CAP reform of 2003 (Ribeiro *et al.* 2014; Santana *et al.* 2014). This is illustrated by the permanent crops, which were only influential after the CAP reform, when they became a dominant land cover type (Ribeiro *et al.* 2014). In contrast, the influence of annual arable crops was only evident in 1995-1997, before their representation in the landscape declined markedly possibly due to the changes associated with the CAP reform (Ribeiro *et al.* 2014). Overall, these results suggest that the influence of different crop types may change over time, and that this may be related to their prevalence across the landscape.

3.5.3 Avian diversity was weakly related to landscape heterogeneity

As expected (Fahrig *et al.* 2011), landscape compositional and configurational heterogeneity had some effects on avian diversity, but these were relatively weak and inconsistent. Nevertheless, there was a tendency in 1995-1997 for total bird diversity increasing with the diversity of crop types, which is consistent with the idea that the presence of different habitats benefits biodiversity by providing conditions for a wide range of species with contrasting ecological requirements (Benton *et al.* 2003; Fuller *et al.* 2004; Fahrig *et al.* 2011). This is also supported to some extent by the positive effects of cover richness and evenness of the natural component on the temporal variation of farmland and steppe bird species richness, though these results are difficult to interpret because these species are mainly associated with crop habitats (Reino *et al.* 2009, 2010; Morgado *et al.* 2010; Moreira *et al*. 2012), and the explanatory power of models including these variables was small (R^2: 0.05-0.12). In contrast to these results, the total species richness in 2010-2012 seemed to be negatively affected by the configurational heterogeneity of the natural component, as there was a positive relation with patch size and a negative relation with patch complexity. This suggests that diversity was benefited by large patches of natural habitat, possibly due to species-area effects (Fischer & Lindenmayer 2002), rather than heterogeneity per se.

The contrast between our results and the importance normally given to heterogeneity on farmland may be a consequence of some particularities of our study, though it may also reflect some general patterns applying to farmland landscapes. First, we used relatively coarse land cover categories, which were designed to have management relevance and to encompass a large pool of bird species with different habitat requirements, though a more detailed habitat categorization might be needed to perceive finer responses to landscape heterogeneity (Fahrig *et al.* 2011). This is supported to some extent by previous studies in our area showing that species richness often peaked close to the edges (Reino *et al.* 2009), and that different habitat types are needed to provide conditions for diverse steppe bird assemblages (Reino *et al.* 2010). Therefore, the influence of heterogeneity may have been underestimated somewhat, though this is unlikely to have affected the strong effects observed for landscape composition. Second, our study may have represented a relatively limited range of variation in landscape heterogeneity, because we sampled areas that were largely dominated by homogeneous open arable land, particularly before the CAP reform of 2003, with virtually no hedgerows and only relatively small woodland and shrubland patches. This may have emphasised the importance of landscape composition, as the production component showed marked spatial and temporal variations (Ribeiro *et al.* 2014). Finally, the results may have been influenced by the particular species pool

occurring in our study area, which included many specialised species associated with large and relatively homogeneous expanses of open farmland habitat (Reino *et al.* 2009, 2010; Morgado *et al.* 2010; Moreira *et al.* 2012), that are typical of similar landscapes across the Iberian Peninsula (e.g., Concepción & Díaz 2011). Therefore, heterogeneity may have had a positive influence on some species but negative on others, thereby reducing its overall effects. Whatever the reasons, however, our results point out that the importance of heterogeneity may vary across farmland landscapes, probably depending on local ecological characteristics and agricultural land uses.

3.6 Conclusions

There are increasing efforts to promote the conservation of biodiversity on farmland while minimising impacts on economic output, and enhancing landscape heterogeneity has been recommended as a key solution to achieve this goal (Fahrig *et al.* 2011). Our results suggest that this option may not be adequate in every case, because farmland diversity in at least some landscapes may be far more affected by the identity of crops produced, rather than by their diversity or spatial configuration. Although this view results from a specific case study focusing on particular ecological and agricultural conditions, it is in line with a wealth of research showing strong links between biodiversity and the type and management of crops (Chamberlain *et al.* 2001; Wilson *et al.* 2005; Stoate *et al.* 2009; Butler *et al.* 2010; Rey 2011; Berg *et al.* 2015; Hiron 2015; Josefsson *et al.* 2016). Therefore, we suggest that the composition of the production component of the landscape needs to be carefully considered when managing farmland for biodiversity, particularly in ours and other open Mediterranean farmland landscapes where there is a range of species tightly associated with crops and pastures for breeding and foraging (Reino *et al.* 2009, 2010; Concepción & Díaz 2011, Moreira *et al.* 2012). In our region, this implies maintaining large areas occupied by rain-fed cereals, fallows and extensive pastureland, which requires agricultural policies and agri-environment subsidy schemes adjusted to local biophysical conditions and market demands (Ribeiro *et al.* 2014, 2016a,b; Santana *et al.* 2014). Overall, we suggest that future studies should explore these ideas in more detail, evaluating under what circumstances major benefits can be achieved by changing landscape heterogeneity (*sensu* Fahrig *et al.* 2011), and where such benefits require focusing primarily on what crops are grown and how they are managed.

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3.8 References

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3.9. Supporting information

Table S3.1 - Percentage of occurrence of bird species recorded in 73 transects sampled annually during the breeding season in southern Portugal, in 1995-1997 and 2010-2012. Species are classified according to their habitat affinities (F – farmland; S – steppe; W – woodland; O - other), conservation status (SPEC #), and phenology (R – resident, M – migratory).

Species[1]	Habitat affinities[2]	Conservation status[3]	Phenology	1995-1997	2010-2012
Galliformes					
Alectoris rufa	F	SPEC 2	R	16.44	47.95
Coturnix coturnix	F, S	SPEC 3	M	54.79	52.05
Ciconiiformes					
Bubulcus ibis	F		R	16.44	10.96
Ciconia nigra	W	SPEC 2	M	1.37	0
Ciconia ciconia	F	SPEC 2	R,M	15.07	32.88
Accipitriformes					
Elanus caeruleus	F	SPEC 3	R	1.37	8.22
Milvus migrans	F	SPEC 3	M	4.11	8.22
Milvus milvus	F	SPEC 2	M	0	2.74
Gyps fulvus	F		R	0	1.37
Circaetus gallicus	W	SPEC 3	M	0	4.11
Circus aeruginosus	O		M	0	2.74
Circus pygargus	F, S		M	23.29	31.51
Buteo buteo	F		R	1.37	12.33
Aquila adalberti	W	SPEC 1	R	0	4.11
Aquila pennata	W	SPEC 3	M	0	1.37
Aquila fasciata	F	SPEC 3	R	0	2.74
Falconiformes					
Falco naumanni	F, S	SPEC 1	M	1.37	27.4
Falco tinnunculus	F	SPEC 3	R	1.37	10.96
Gruiformes					
Tetrax tetrax	F, S	SPEC 1	R	54.79	56.16
Otis tarda	F, S	SPEC 1	R	19.18	23.29
Charadriiformes					
Burhinus oedicnemus	F, S	SPEC 3	R	8.22	21.92
Glareola pratincola	F, S	SPEC 3	M	0	1.37
Pteroclidiformes					
Pterocles orientalis	F, S	SPEC 2	R	0	12.33
Columbiformes					
Columba livia	F		R	0	2.74
Columba palumbus	W		R	0	12.33
Streptopelia decaocto	F		R	0	21.92
Streptopelia turtur	F	SPEC 3	M	0	1.37
Cuculiformes					
Clamator glandarius	F		M	1.37	8.22
Cuculus canorus	F		M	5.48	6.85
Strigiformes					
Athene noctua	F	SPEC 3	R	5.48	6.85
Coraciiformes					
Merops apiaster	F	SPEC 3	M	12.33	52.05

Species[1]	Habitat affinities[2]	Conservation status[3]	Phenology	1995-1997	2010-2012
Coracias garrulus	F, S	SPEC 2	M	0	4.11
Upupa epops	F	SPEC 3	M	24.66	26.03
Piciformes					
Dendrocopos major	W		R	0	1.37
Passeriformes					
Melanocorypha calandra	F, S	SPEC 3	R	30.14	36.99
Calandrella brachydactyla	F, S	SPEC 3	M	38.36	34.25
Galerida spp. *	F, S	SPEC 3	R	21.92	75.34
Lullula arborea	W	SPEC 2	R	10.96	9.59
Hirundo rustica	F	SPEC 3	M	19.18	43.84
Cecropis daurica	F		M	0	4.11
Delichon urbicum	F	SPEC 3	M	0	5.48
Anthus campestris	F, S	SPEC 3	M	4.11	20.55
Motacilla flava	F		M	0	4.11
Motacilla alba	F		R	1.37	1.37
Cercotrichas galactotes	W	SPEC 3	M	0	1.37
Luscinia megarhynchos	W		M	4.11	15.07
Saxicola rubicola	F		R	19.18	35.62
Oenanthe hispanica	F, S	SPEC 2	M	13.7	21.92
Turdus viscivorus	W		R	0	1.37
Turdus merula	W		R	8.22	34.25
Cettia cetti	W		R	4.11	4.11
Cisticola juncidis	F, S		R	65.75	80.82
Acrocephalus scirpaceus	O		M	0	1.37
Acrocephalus arundinaceus	O		M	0	1.37
Hippolais polyglotta	W		M	0	2.74
Sylvia atricapilla	W		R	0	1.37
Sylvia hortensis	F	SPEC 3	M	0	1.37
Sylvia undata	W	SPEC 2	R	0	2.74
Sylvia cantillans	W		M	0	2.74
Sylvia melanocephala	W		R	12.33	15.07
Phylloscopus ibericus	W		M	0	1.37
Phyloscopus collybita	W		M	0	1.37
Aegithalos caudatus	W		R	1.37	0
Cyanistes caeruleus	W		R	8.22	13.7
Parus major	W		R	12.33	10.96
Certhia brachydactyla	W		R	2.74	8.22
Oriolus oriolus	W		M	0	1.37
Lanius meridionalis	F		R	12.33	20.55
Lanius senator	F	SPEC 2	M	15.07	8.22
Garrulus glandarius	W		R	0	4.11
Cyanopica cyanus	W		R	0	21.92
Pica pica	F		R	0	10.96
Corvus monedula	F		R	0	2.74
Corvus corone	F		R	0	26.03
Corvus corax	W		R	4.11	4.11
Sturnus unicolor	F		R	9.59	28.77
Passer spp.**	F		R	8.22	34.25
Fringila coelebs	W		R	2.74	1.37

Species[1]	Habitat affinities[2]	Conservation status[3]	Phenology	1995-1997	2010-2012
Serinus serinus	F		R	0	4.11
Chloris chloris	F		R	4.11	20.55
Carduelis carduelis	F		R	5.48	49.32
Carduelis cannabina	F	SPEC 2	R	0	23.29
Estrilda astrild	O		R	0	1.37
Emberiza calandra	F, S	SPEC 2	R	94.52	93.15

[1] Species are listed in taxonomic order following Equipa Atlas (2008).

[2] Bird habitat categorizations based on Ehrlich *et al.* (1994), Suárez *et al.* (1997), Equipa Atlas (2008), Reino *et al.* (2009) and EBCC (2012).

[3] Species of European Conservation Concern: SPEC 1 - Species of global conservation concern; SPEC 2 - species concentrated in Europe and with an unfavorable conservation status; SPEC 3 - species not concentrated in Europe but with an unfavorable conservation status (BirdLife International 2004).

* *Galerida* spp.: includes *Galerida theklae*, *G. cristata* and *Galerida* sp. observations.

** *Passer* spp.: includes *Passer domesticus*, *P. hispaniolensis* and *Passer* sp. observations. We have not considered *Passe*r spp. as a SPEC species because most of the identified records were from *P. hispaniolensis*.

Table S3.2 - Description of variables used to quantify landscape compositional and configurational heterogeneity in 250-m buffers around 73 transects used to estimate bird species richness in 1995-1997 and 2010-2012, in southern Portugal.

Landscape variable (unit, abbreviation)	Description
Compositional heterogeneity	
Land cover richness (no., CR)	Total number of different natural/production land cover types.
Land cover diversity (SHDI)[a]	Shannon's diversity index computed on the proportion of different natural/production land cover types.
Land cover evenness (SHEI) [b]	Shannon's evenness index computed on the proportion of different natural/production land cover types.
Configurational heterogeneity	
Largest patch index (%, LPI)	Percentage of area of the largest natural/production land cover type patch.
Patch size (ha, AREA)	Mean area of natural/production land cover type patches.
Edge density (m^2/ha, ED)	Density of edges between natural and production land cover type patches.
Shape complexity (SHAPE)	Mean perimeter-to-area ratio of natural/production land cover type patches.

[a]SHDI = 0 when the landscape contains only 1 or 0 cover types;

[b]SHEI = 0 when the landscape contains only 1 or 0 cover types. SHEI = 1 when distribution of area among patch types is perfectly even (i.e., proportional abundances are the same).

Table S3.3 - Formulation of candidate models (g_{1-63}) based on all possible combinations of the six sets of landscape variables listed in Table S3.1.

No. variable sets	No. models	Model formulation
One set	6	g_1 = Set 1
		g_2 = Set 2
		g_3 = Set 3
		g_4 = Set 4
		g_5 = Set 5
		g_6 = Set 6
Two sets	15	g_7 = Set 1 + Set 2
		g_8 = Set 1 + Set 3
		g_9 = Set 1 + Set 4
		g_{10} = Set 1 + Set 5
		g_{11} = Set 1 + Set 6
		g_{12} = Set 2 + Set 3
		g_{13} = Set 2 + Set 4
		g_{14} = Set 2 + Set 5
		g_{15} = Set 2 + Set 6
		g_{16} = Set 3 + Set 4
		g_{17} = Set 3 + Set 5
		g_{18} = Set 3 + Set 6
		g_{19} = Set 4 + Set 5
		g_{20} = Set 4 + Set 6
		g_{21} = Set 5 + Set 6
Three sets	20	g_{22} = Set 1 + Set 2 + Set 3
		g_{23} = Set 1 + Set 2 + Set 4
		g_{24} = Set 1 + Set 2 + Set 5
		g_{25} = Set 1 + Set 2 + Set 6
		g_{26} = Set 1 + Set 3 + Set 4
		g_{27} = Set 1 + Set 3 + Set 5
		g_{28} = Set 1 + Set 3 + Set 6
		g_{29} = Set 1 + Set 4 + Set 5
		g_{30} = Set 1 + Set 4 + Set 6
		g_{31} = Set 1 + Set 5 + Set 6
		g_{32} = Set 2 + Set 3 + Set 4
		g_{33} = Set 2 + Set 3 + Set 5
		g_{34} = Set 2 + Set 3 + Set 6
		g_{35} = Set 2 + Set 4 + Set 5
		g_{36} = Set 2 + Set 4 + Set 6
		g_{37} = Set 2 + Set 5 + Set 6
		g_{38} = Set 3 + Set 4 + Set 5
		g_{39} = Set 3 + Set 4 + Set 6
		g_{40} = Set 3 + Set 5 + Set 6
		g_{41} = Set 4 + Set 5 + Set 6
Four sets	15	g_{42} = Set 1 + Set 2 + Set 3 + Set 4
		g_{43} = Set 1 + Set 2 + Set 3 + Set 5
		g_{44} = Set 1 + Set 2 + Set 3 + Set 6
		g_{45} = Set 1 + Set 2 + Set 4 + Set 5
		g_{46} = Set 1 + Set 2 + Set 4 + Set 6
		g_{47} = Set 1 + Set 2 + Set 5 + Set 6

No. variable sets	No. models	Model formulation
Four sets (cont.)		g_{48} = Set 1 + Set 3 + Set 4 + Set 5
		g_{49} = Set 1 + Set 3 + Set 4 + Set 6
		g_{50} = Set 1 + Set 3 + Set 5 + Set 6
		g_{51} = Set 1 + Set 4 + Set 5 + Set 6
		g_{52} = Set 2 + Set 3 + Set 4 + Set 5
		g_{53} = Set 2 + Set 3 + Set 4 + Set 6
		g_{54} = Set 2 + Set 3 + Set 5 + Set 6
		g_{55} = Set 2 + Set 4 + Set 5 + Set 6
		g_{56} = Set 3 + Set 4 + Set 5 + Set 6
Five sets	6	g_{57} = Set 1 + Set 2 + Set 3 + Set 4 + Set 5
		g_{58} = Set 1 + Set 2 + Set 3 + Set 4 + Set 6
		g_{59} = Set 1 + Set 2 + Set 3 + Set 5 + Set 6
		g_{60} = Set 1 + Set 2 + Set 4 + Set 5 + Set 6
		g_{61} = Set 1 + Set 3 + Set 4 + Set 5 + Set 6
		g_{62} = Set 2 + Set 3 + Set 4 + Set 5 + Set 6
Six sets	1	g_{63} = Set 1 + Set 2 + Set 3 + Set 4 + Set 5 + Set 6

Table S3.4 - Summary of average models relating spatial variation in bird species richness in 1995-1997 to landscape variables. In each case we provide the model-averaged partial standardized coefficients (Coef) and their partial standardized standard error (SE). The relative importance of each variable in the model (Imp) was calculated as the ratio between the respective partial standardized coefficient and the largest standardized coefficient in the model (Cade 2015). Variables are ordered by their relative importance within each model. Variables with Imp > 0.4 are in bold, and the ones with negative effects are underlined. See main text for methodological details.

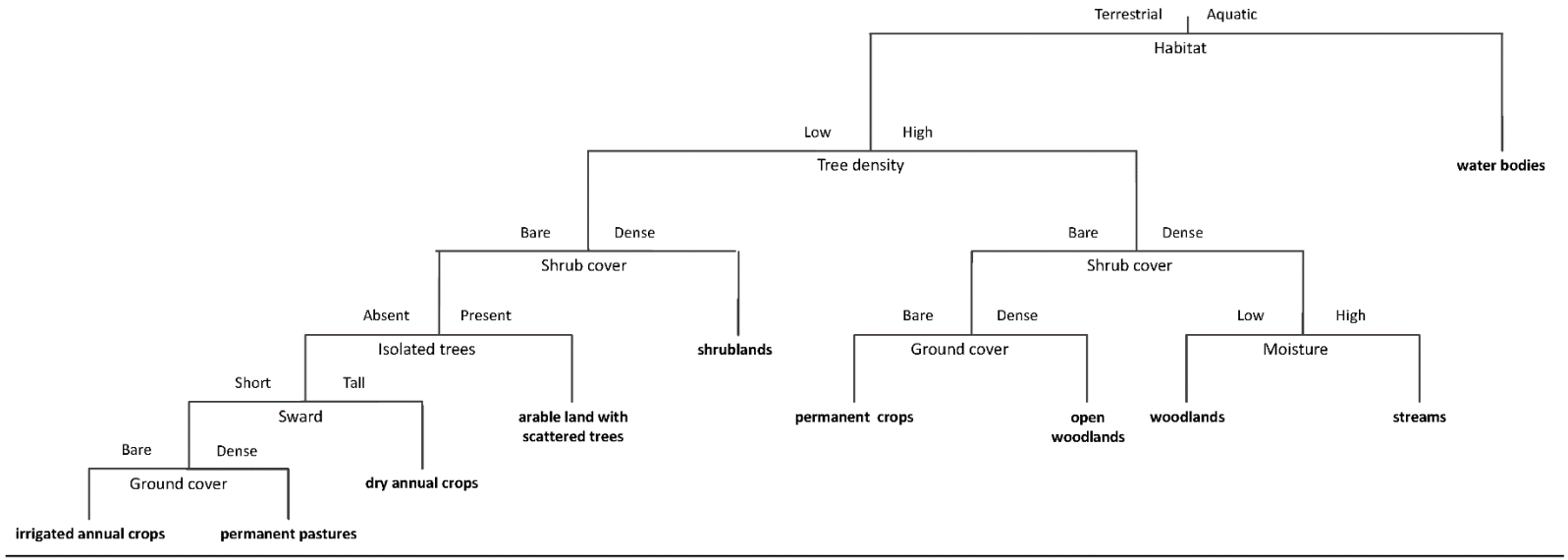
Variable set	Landscape variable	Coef	SE	Imp
All species (R^2 = 0.58)				
Composition/Production	**Arable land with scattered trees**	**-0.33**	**0.06**	**1.00**
Composition/Production	**Irrigated annual crops**	**-0.30**	**0.06**	**0.91**
Composition/Production	**Annual dry crops**	**-0.23**	**0.05**	**0.70**
Composition/Production	**Permanent pastures**	**-0.18**	**0.05**	**0.55**
Compositional heterogeneity/Production	**Cover diversity (Production)**	**0.14**	**0.06**	**0.43**
Composition/Production	**Permanent crops**	**-0.14**	**0.06**	**0.42**
Compositional heterogeneity/Production	Cover evenness (Production)	-0.10	0.06	0.31
Compositional heterogeneity/Production	Cover richness (Production)	0.00	0.03	0.00
Woodland birds (R^2 = 0.78)				
Composition/Natural	**Open woodland**	**0.71**	**0.11**	**1.00**
Composition/Natural	**Woodland**	**0.43**	**0.07**	**0.61**
Composition/Natural	Water bodies	-0.08	0.15	0.11
Composition/Natural	Streams	0.04	0.08	0.06
Composition/Natural	Shrubland	0.03	0.08	0.04
Farmland birds (R^2 = 0.39)				
Composition/Production	**Arable land with scattered trees**	**-0.24**	**0.07**	**1.00**
Composition/Production	**Annual irrigated crops**	**-0.17**	**0.07**	**0.72**
Compositional heterogeneity/Production	Cover diversity (Production)	0.09	0.07	0.37
Compositional heterogeneity/Production	Cover evenness (Production)	-0.06	0.07	0.23
Composition/Production	Permanent crops	-0.04	0.06	0.18
Composition/Production	Dry annual crops	-0.03	0.05	0.12
Composition/Production	Permanent pastures	0.01	0.03	0.02
Compositional heterogeneity/Production	Cover richness (Production)	-0.01	0.04	0.02
Steppe birds (R^2 = 0.31)				
Composition/Production	**Permanent pastures**	**0.19**	**0.07**	**1.00**
Composition/Production	**Annual dry crops**	**0.19**	**0.06**	**0.99**
Composition/Production	Arable land with scattered trees	-0.03	0.06	0.15
Composition/Production	Annual irrigated crops	0.01	0.04	0.06
Composition/Production	Permanent crops	0.01	0.04	0.06

Table S3.5 - Summary of average models relating spatial variation in bird species richness in 2010-2012 to landscape variables. In each case we provide the model-averaged partial standardized coefficients (Coef) and their partial standardized standard error (SE). The relative importance of each variable in the model (Imp) was calculated as the ratio between the respective partial standardized coefficient and the largest standardized coefficient in the model (Cade 2015). Variables are ordered by their relative importance within each model. Variables with Imp > 0.4 are in bold, and the ones with negative effects are underlined. See main text for methodological details.

Variable set	Landscape variable	Coef	SE	Imp
All species (R^2 = 0.38)				
Composition/Natural	**Streams**	**0.08**	**0.04**	**1.00**
Configurational heterogeneity/Natural	**Shape complexity (Natural)**	**-0.05**	**0.05**	**0.61**
Configurational heterogeneity/Natural	**Patch size (Natural)**	**0.04**	**0.04**	**0.44**
Configurational heterogeneity/Natural	Large patch index (Natural)	0.03	0.04	0.33
Composition/Natural	Woodland	0.02	0.03	0.28
Composition/Natural	Open woodland	-0.02	0.04	0.27
Composition/Natural	Shrubland	0.02	0.03	0.22
Configurational heterogeneity/Natural	Edge density (Natural)	0.01	0.03	0.07
Composition/Natural	Water bodies	0.00	0.02	0.03
Woodland (R^2 = 0.76)				
Composition/Production	**Permanent pastures**	**-0.66**	**0.26**	**1.00**
Composition/Production	**Annual dry crops**	**-0.40**	**0.21**	**0.61**
Configurational heterogeneity/Natural	Patch size (Natural)	0.26	0.11	0.39
Composition/Natural	Woodland	0.17	0.11	0.26
Composition/Natural	Shrubland	0.16	0.11	0.24
Composition/Natural	Water bodies	-0.12	0.11	0.18
Composition/Natural	Open woodland	-0.10	0.10	0.15
Composition/Natural	Streams	0.07	0.10	0.11
Composition/production	Arable land with scattered trees	0.05	0.09	0.08
Composition/production	Permanent crops	0.05	0.15	0.07
Configurational heterogeneity/Natural	Large patch index (Natural)	0.02	0.08	0.03
Composition/Production	Annual irrigated crops	-0.01	0.09	0.02
Configurational heterogeneity/Natural	Shape complexity (Natural)	0.01	0.06	0.02
Configurational heterogeneity/Natural	Edge density (Natural)	0.01	0.06	0.01
Farmland (R^2 = 0.15)				
Configurational heterogeneity/Production	**Production edge density**	**0.09**	**0.05**	**1.00**
Configurational heterogeneity/Production	Mean production shape complexity	0.00	0.02	0.03
Configurational heterogeneity/Production	Largest production patch index	0.00	0.02	0.03
Configurational heterogeneity/Production	Mean patch area	0.00	0.02	0.03
Steppe (R^2 = 0.29)				
Composition/Production	**Permanent pastures**	**0.17**	**0.06**	**1.00**
Composition/Production	**Annual dry crops**	**0.14**	**0.06**	**0.79**
Composition/Production	Annual irrigated crops	0.03	0.05	0.16
Composition/Production	Arable land with scattered trees	0.02	0.04	0.14
Composition/Production	Permanent crops	0.00	0.04	0.01

Table S3.6 - Summary of average models relating temporal variation in bird species richness to landscape variables. In each case we provide the model-averaged partial standardized coefficients (Coef) and their partial standardized standard error (SE). The relative importance of each variable in the model (Imp) was calculated as the ratio between the respective partial standardized coefficient and the largest standardized coefficient in the model (Cade 2015). Variables are ordered by their relative importance within each model. Variables with Imp > 0.4 are in bold, and the ones with negative effects are underlined. See main text for methodological details.

Variable set	Landscape variable	Coef	SE	Imp
All species (R^2 = 0.17)				
Composition/production	**Permanent crops**	**1.06**	**0.67**	**1.00**
Composition/production	**Arable land with scattered trees**	**-0.65**	**0.63**	**0.61**
Composition/production	Permanent pastures	-0.09	0.35	0.09
Composition/production	Annual dry crops	0.06	0.35	0.06
Composition/production	Annual irrigated crops	0.02	0.30	0.02
Woodland (R^2 = 0.25)				
Composition/production	**Permanent crops**	**0.62**	**0.26**	**1.00**
Composition/production	Permanent pastures	-0.13	0.21	0.21
Composition/production	Arable land with scattered trees	-0.08	0.15	0.13
Composition/production	Annual dry crops	0.05	0.20	0.08
Composition/production	Annual irrigated crops	-0.03	0.14	0.05
Farmland (R^2 = 0.05)				
Compositional heterogeneity/Natural	**Cover evenness (Natural)**	**0.56**	**0.56**	**1.00**
Compositional heterogeneity/Natural	Cover diversity (Natural)	0.09	0.41	0.17
Compositional heterogeneity/Natural	Cover richness (Natural)	0.00	0.25	0.00
Steppe (R^2 = 0.12)				
Compositional heterogeneity/Natural	**Cover richness (Natural)**	**0.37**	**0.35**	**1.00**
Compositional heterogeneity/Natural	**Cover evenness (Natural)**	**0.28**	**0.33**	**0.75**
Compositional heterogeneity/Natural	Cover diversity (Natural)	0.03	0.24	0.07



Natural component	
woodlands	= holm woods (*Quercus rotundifolia*) with >30% tree cover and shrub understory; old eucalyptus plantations with understory; tree lines
open woodlands	= holm woods with >30% tree cover and grassy understory, young plantations without understory
shrublands	= shrublands without trees or with scattered trees
streams	= streams with vegetation (herbs, shrubs or trees)
water bodies	= ponds and reservoirs
Production component	
arable land with scattered trees	= annual crops with scattered trees (<30% tree cover)
dry annual crops	= non-irrigated annual crops (dry cereals (e.g. wheat, barley) and legumes) in rotation with ploughed fields, stubbles and fallows usually grazed by sheep or cattle
permanent pastures	= grassy vegetation grazed by sheep or cattle
irrigated annual crops	= irrigated annual crops (corn and sunflower)
permanent crops	= permanent irrigated and non-irrigated crops (olive groves and vineyards)

Fig. S3.1 **-** Classification tree of land cover categories used to model the relations between bird species richness and landscape characteristics in southern Portugal. Categories were defined considering the main nesting and foraging habitats of bird species in the study area (Moreira 1999; Delgado & Moreira 2000; Stoate *et al.* 2000; Reino *et al.* 2009, 2010), and assuming that habitat preferences are often influenced strongly by structural characteristics (e.g. tree density, shrub cover, sward density and height, and amount of bare ground – ground cover). Characteristics of the herbaceous sward were considered during the sampling months (April-May), though they are known to vary strongly during the annual cycle (e.g., dry annual crops are sown in autumn and thus the sward is tall and dense during the breeding season, whereas irrigated annual crops are generally sown in spring, and so during the breeding season the sward tends to be short, sparse, and with a high proportion of bare ground).

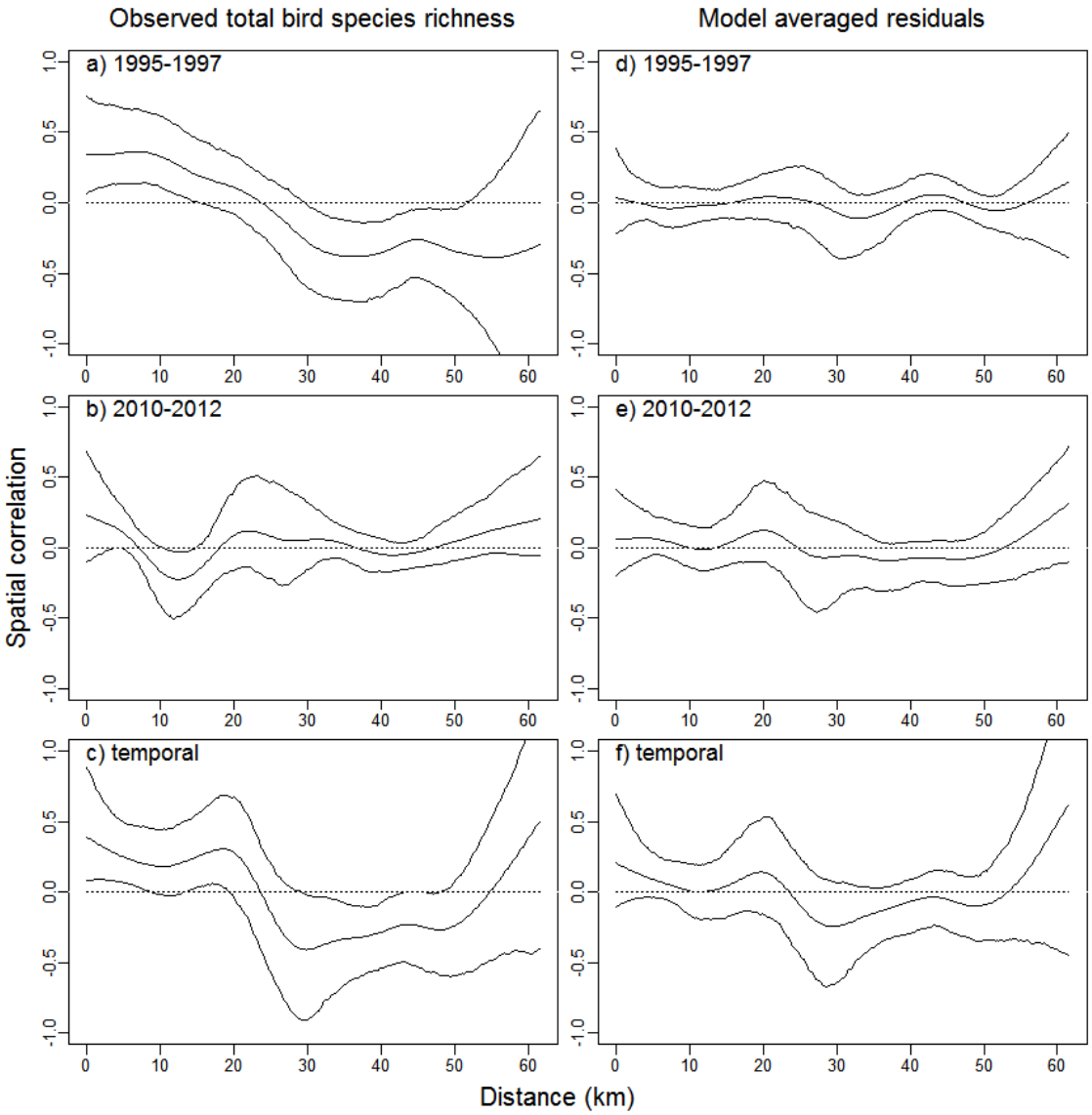


Fig. S3.2 - Spline correlograms describing spatial autocorrelation for total bird species richness and for the residuals of models relating species richness to landscape variables (Tables S3.4 – S3.6). Separate correlograms are presented for 1995-97 (a, d), 2010-12 (b, e), and temporal variation (c, f). Lines represent the estimate (in the middle) and the 95% confidence envelopes (external lines) using 1000 bootstrap resamples (Bjørnstad & Falck 2001).

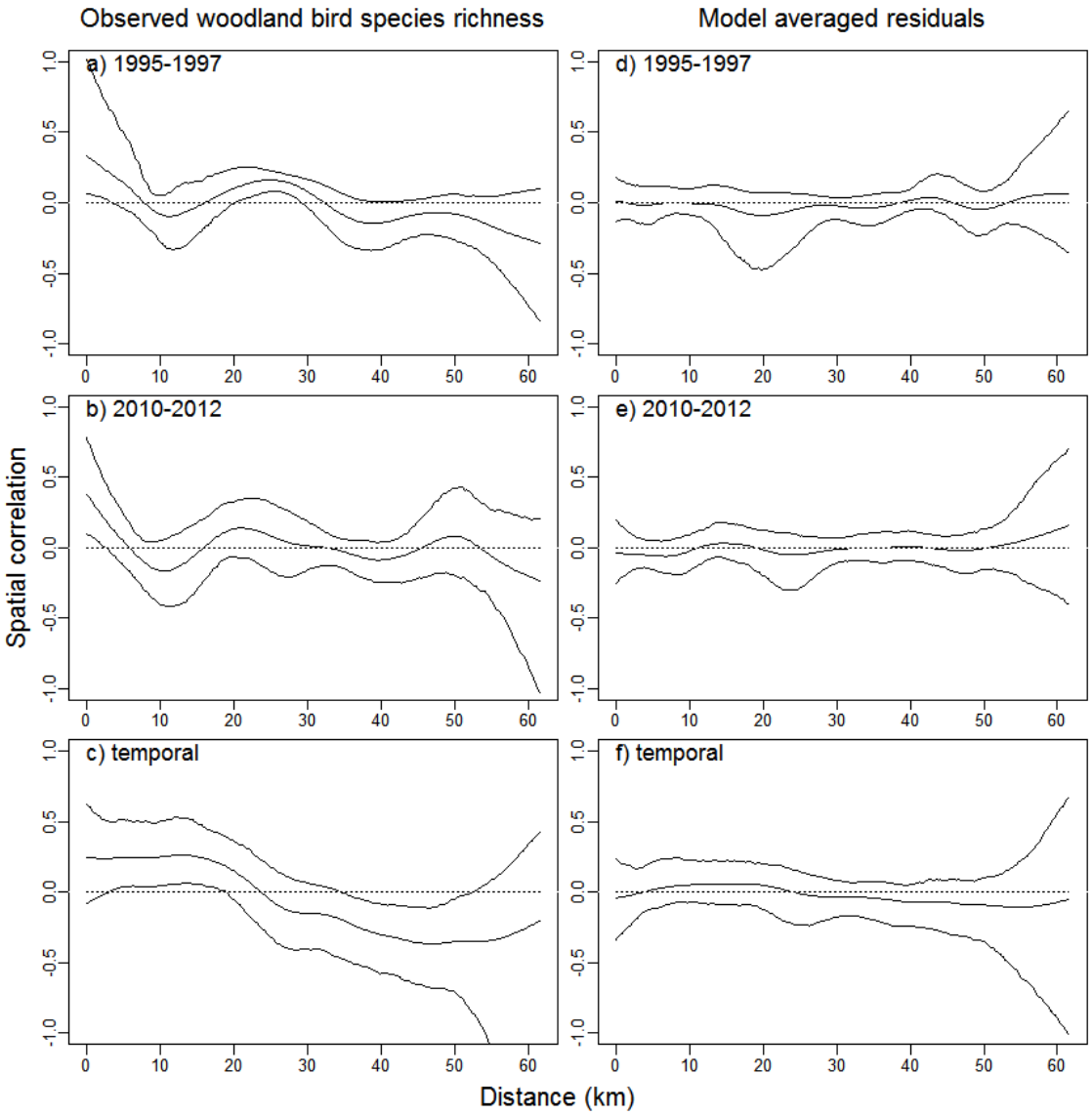


Fig. S3.3 - Spline correlograms describing spatial autocorrelation for woodland bird species richness and for the residuals of models relating species richness to landscape variables (Tables S3.4 – S3.6). Separate correlograms are presented for 1995-97 (a, d), 2010-12 (b, e), and temporal variation (c, f). Lines represent the estimate (in the middle) and the 95% confidence envelopes (external lines) using 1000 bootstrap resamples (Bjørnstad & Falck 2001).

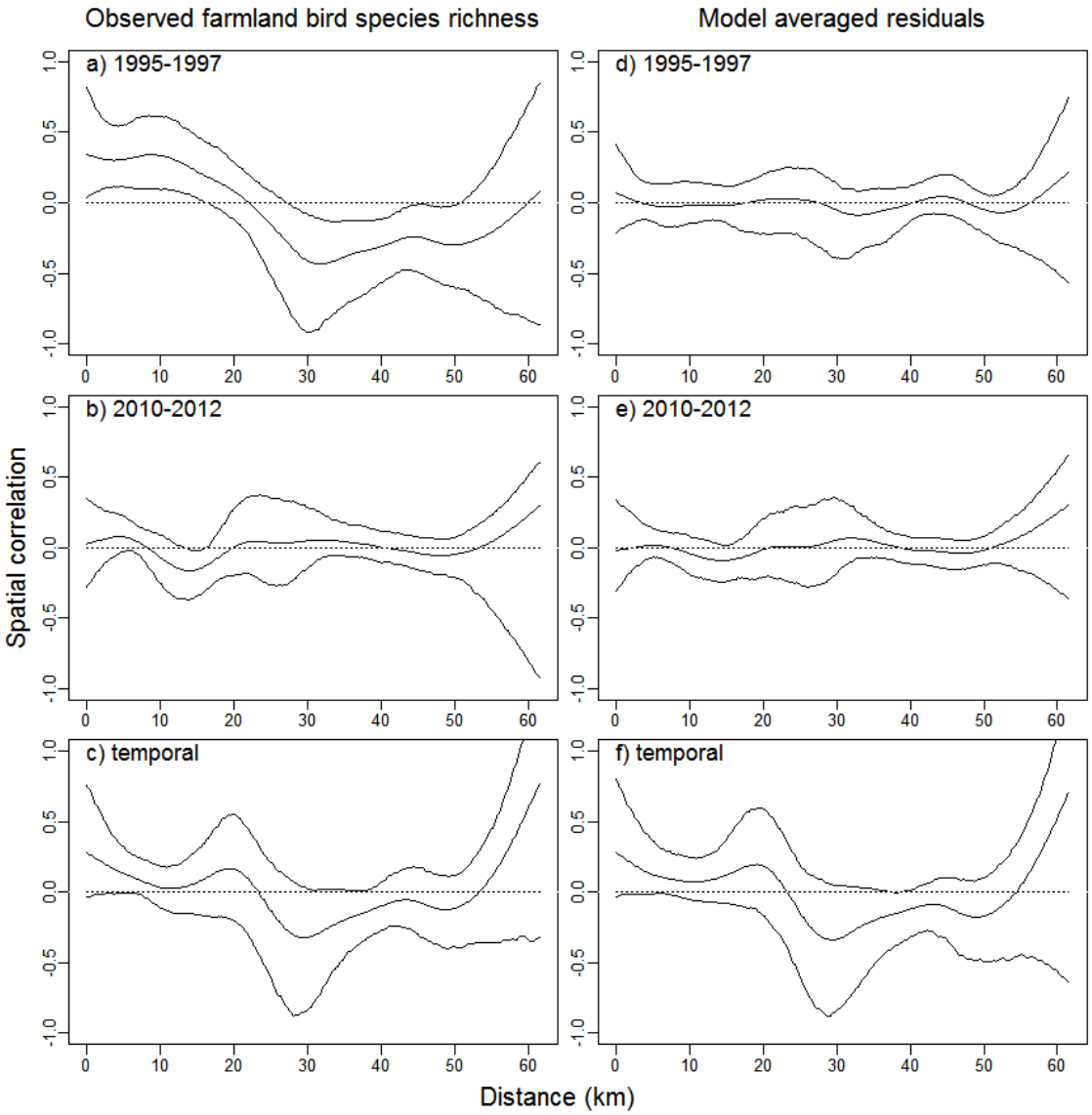


Fig. S3.4 - Spline correlograms describing spatial autocorrelation for farmland bird species richness and for the residuals of models relating species richness to landscape variables (Tables S3.4 – S3.6). Separate correlograms are presented for 1995-97 (a, d), 2010-12 (b, e), and temporal variation (c, f). Lines represent the estimate (in the middle) and the 95% confidence envelopes (external lines) using 1000 bootstrap resamples (Bjørnstad & Falck 2001).

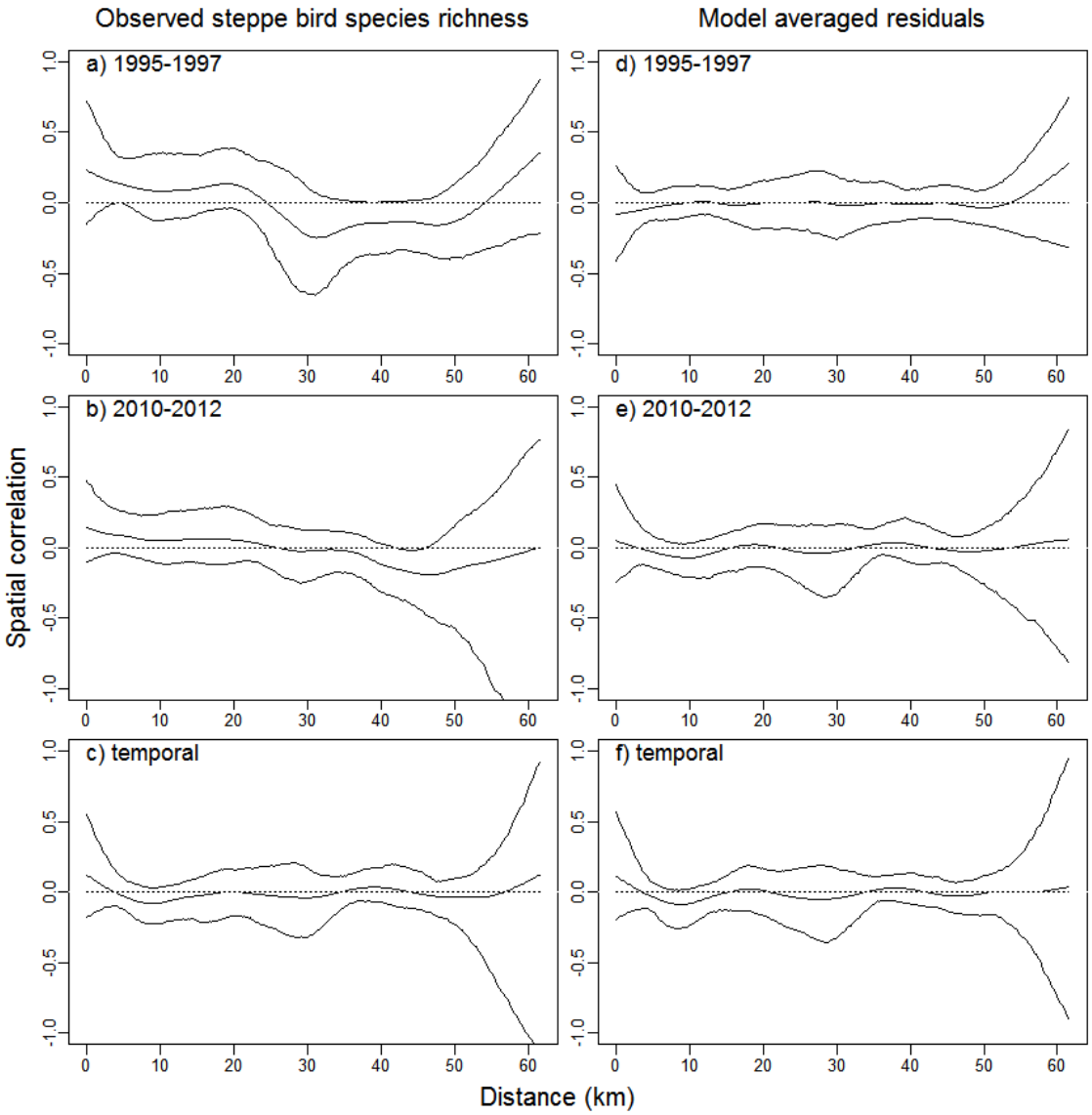


Fig. S3.5 - Spline correlograms describing spatial autocorrelation for steppe bird species richness and for the residuals of models relating species richness to landscape variables (Tables S3.4 – S3.6). Separate correlograms are presented for 1995-97 (a, d), 2010-12 (b, e), and temporal variation (c, f). Lines represent the estimate (in the middle) and the 95% confidence envelopes (external lines) using 1000 bootstrap resamples (Bjørnstad & Falck 2001).

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Chapter 4

Using beta diversity to inform agricultural policies and conservation actions on Mediterranean farmland

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4. Using beta diversity to inform agricultural policies and conservation actions on Mediterranean farmland

4.1 Summary

1. Spatial variation in species composition (β-diversity) is an important component of farmland biodiversity, which together with local richness (α-diversity) drives the number of species in a region (γ-diversity). However, β-diversity is seldom used to inform conservation, due to limited understanding of its responses to agricultural management, and lack of clear links between β-diversity changes and conservation outcomes.

2. We explored the value of β-diversity to guide conservation on farmland, by quantifying the contribution of bird α- and β-diversity to γ-diversity variation in low- and high-intensity Mediterranean farmland, before (1995–1997) and after (2010–2012) the Common Agricultural Policy reform of 2003. We further related β-diversity to landscape heterogeneity, and assessed the conservation significance of β-diversity changes.

3. In 1995–1997, bird diversity was highest in low-intensity farmland, where it further increased in 2010–2012 due to a strong positive contribution of α-diversity to γ-diversity. In high-intensity farmland, diversity converged over time to much the same values of low-intensity farmland, with strong positive contributions of both α- and β-diversity. These patterns were largely consistent for total, farmland and species of European conservation concern assemblages, and less so for steppe birds.

4. Beta diversity increased with landscape heterogeneity, particularly related to spatial gradients from agricultural to natural habitats in low-intensity farmland, and from annual to permanent crops (olive groves) in high-intensity farmland. The first gradient was associated with the replacement of steppe birds of high conservation concern by more generalist species, while the second was associated with the replacement between species with lower or higher affinity for woodland and shrubland habitats.

5. *Synthesis and applications.* In low-intensity farmland, spatial variation in species composition (β-diversity) was largely stable over time, reflecting a positive conservation outcome related to persistence of landscape heterogeneity patterns required by endangered steppe bird species. In contrast, β-diversity in high-intensity farmland was favoured by increases in landscape heterogeneity driven by olive grove

expansion, contributing to enhancement of total bird diversity. Overall, our results stress the value of β-diversity to understand impacts of agricultural policies and conservation actions, but also highlight the need to evaluate β-diversity changes against specific conservation goals.

4.2 Introduction

The effects of human activities on biodiversity are generally assessed by estimating trends in local species richness (alpha diversity, α, *sensu* Whittaker 1960) for particular species assemblages (Newbold *et al.* 2015). However, this metric provides only a partial view of biodiversity change, because the total number of species represented in a region (i.e. gamma diversity, γ) is shaped by both α-diversity and by variation in species composition among sites (beta diversity, β) (Whittaker 1960). Therefore, examining trends in β-diversity may be useful to understand the impacts of anthropogenic drivers whose effects on γ-diversity may not be adequately captured by α-diversity alone (Socolar *et al*. 2016). For instance, land-use changes increasing habitat diversity may increase β-diversity due to species replacement among sites with different habitats (i.e. the replacement component of β-diversity, β_{Repl}; Legendre 2014), and thus increase γ-diversity without necessarily changing α-diversity (Gaston *et al.* 2007; Monnet *et al.* 2014). Alternatively, land-use changes affecting habitat attributes may cause variation in the number of species among sites with different habitat characteristics (i.e. the richness difference component of β-diversity, $\beta_{RichDiff}$; Legendre 2014), without necessarily affecting β_{Repl}. In this case, the contribution of β-diversity to γ-diversity will likely be relatively small, and local factors affecting α-diversity may be particularly relevant. There is thus a need to consider β-diversity and its components, β_{Repl} and $\beta_{RichDiff}$, in conservation research to understand biodiversity changes and their underlying ecological mechanisms (Socolar *et al.* 2016; Żmihorski *et al.* 2016).

On farmland, the diversity and spatial arrangement of habitats (i.e. landscape heterogeneity) are widely recognised as key for biodiversity conservation (Benton, Vickery & Wilson 2003; Fahrig *et al.* 2011; but see Báldi & Batáry 2011). Loss of heterogeneity due for instance to crop specialization, loss of crop rotations, enlargement of fields, and loss of non-crop habitats (e.g. woodland patches, scattered trees, hedgerows, and ponds), is a dominant driver of farmland biodiversity declines (e.g. Benton *et al.* 2003). As a consequence, agri-environment schemes and other agricultural policies aim to maintain or restore landscape heterogeneity, though their actual biodiversity benefits remain disputed (Stoate *et al.* 2009; Batáry *et al.* 2015). A few studies have used β-diversity to address these issues, providing evidence that β-diversity

was lower in intensive than in extensive farmland (Ekroos *et al.* 2010; Flohre *et al.* 2011; Karp *et al.* 2012), and in conventional than in organic farms (Gabriel *et al.* 2006; Clough *et al.* 2007), though the patterns observed varied across spatial scales, taxa and functional groups. However, to the best of our knowledge no study has yet evaluated how β-diversity varies through time in response to changes in agricultural policies and conservation actions, though understanding this variation would be relevant for improving agricultural policies, land planning and conservation management prescriptions to reverse farmland biodiversity loss.

Here, we address these issues by quantifying the patterns and correlates of farmland bird diversity during a period of major land-use change. We focused on two contrasting areas in southern Portugal, one of which was a Special Protection Area (SPA) representative of low-intensity farmland and holding internationally important steppe bird populations, while the other was a nearby high-intensity farmland area (Ribeiro *et al.* 2014; Santana *et al.* 2014, 2017a). The study was conducted before (1995–1997) and after (2010–2012) the Common Agricultural Policy (CAP) reform of 2003, which in our area was associated with marked expansions in land uses previously scarce in the region (Ribeiro *et al.* 2014), and with significant increases in α-diversity of breeding birds due primarily to increases in species that benefited from woodland and shrubland habitats and olive groves (Santana *et al.* 2014, 2017a). We hypothesize that these changes should also have affected γ-diversity, both due to the observed increases in α-diversity, and because likely increases in landscape heterogeneity should have contributed to increasing species replacement (β_{Repl}) and thus overall β-diversity. However, we also hypothesize that the effects of heterogeneity on diversity probably varied across species groups, because while some species are favoured by heterogeneity (Fahrig *et al.* 2011), others such as steppe birds are associated with relatively homogeneous landscapes (Báldi & Batáry 2011). To test these ideas, we examined: (i) temporal trends in landscape heterogeneity and the contribution of specific land uses to such trends; (ii) temporal trends in bird diversity and the contribution of α- and β-diversity to γ-diversity; (iii) the relations between β-diversity and landscape heterogeneity; and (iv) the identity of species contributing most to the relations between β-diversity and landscape heterogeneity. Results were used to discuss the value and limitations of β-diversity to inform conservation management on farmland.

4.3 Materials and methods

4.3.1 Study area

The study was conducted in southern Portugal, within a low-intensity farmland area included in the Special Protection Area (SPA) of Castro Verde (37º 41´ N, 8º 00´ W), and within the nearby (about 10-km distant) high-intensity farmland area of Ferreira do Alentejo (38º 03´ N, 8º 06´ W) (Fig. 4.1). The low-intensity area was dominated for decades by a traditional farming system characterised by the rotation of rain-fed cereals and fallows typically grazed by sheep, which provide habitat for steppe bird species of conservation concern (Delgado & Moreira 2000; Santana *et al.* 2014). To preserve this system, a voluntary agri-environment scheme was established in 1995, while legal regulations setting restrictions to afforestation, the development of irrigation infrastructures, and the expansion of permanent crops were established after the creation of the SPA in 1999 (Ribeiro *et al*. 2014). Furthermore, there were conservation projects targeting mainly great bustard *Otis tarda*, little bustard *Tetrax tetrax* and lesser kestrel *Falco naumanni*, which included the purchase and management of critical areas, and improvement of breeding and foraging habitats (Santana *et al.* 2014 and references within). Despite these interventions, over the last decade there were marked shifts from the traditional system towards the specialized production of either cattle or sheep, with declines in cereal and fallow land, and increases in pastures (Ribeiro *et al.* 2014). This probably resulted from the decoupling of payments from production introduced by the CAP reform of 2003 (i.e. farmers were no longer required to maintain production for receiving CAP payments), as arable crops were completely decoupled while sheep and suckler cows remained partially and fully coupled, respectively (Ribeiro *et al.* 2014). The high-intensity farmland contrasted markedly to the SPA, because it had irrigation infrastructures, better soils, and no constraints to crop conversion (Ribeiro *et al.* 2014). At beginning of the study this farmland area mainly produced irrigated annual crops, but thereafter there was a major shift towards the production of permanent crops (mainly olive groves) (Ribeiro *et al.* 2014).

4.3.2 Sampling design

The study was based on a network of 250-m transects established in 1995, where birds were counted annually in 1995–1997 and 2010–2012, thus covering periods before and after the CAP reform of 2003 and the development of steppe bird conservation programs (Stoate *et al.* 2003; Santana *et al.* 2014). These transects were initially designed to evaluate the effects of an agri-environment scheme (Stoate *et al.* 2003), with 46 transects set in the SPA and 32 in a nearby high-intensity farmland area (Santana *et al.*

2014). From these, we retained 43 transects in low-intensity and 30 transects in high-intensity farmland that were surveyed in at least two years in each period (Santana *et al.* 2017a). Transects followed a random bearing, and they started at grid intersections of a 1-km square grid overlaid on the study area, which were selected based on access constraints and the presence of agricultural land uses (Stoate *et al.* 2003).

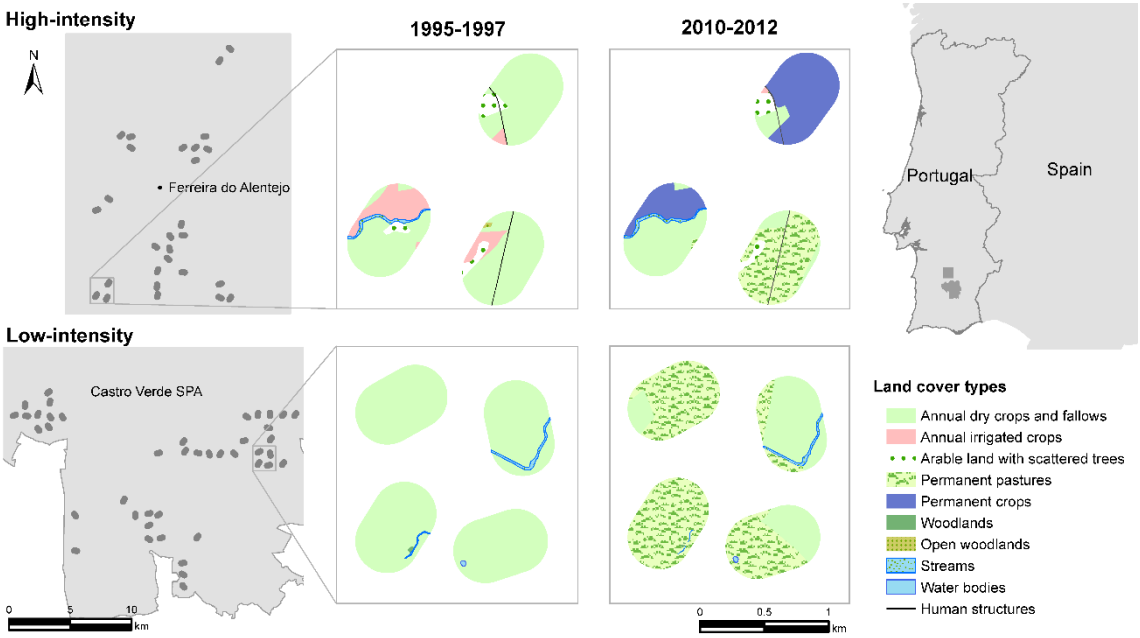

Fig. 4.1 - Location of the study area in Southern Portugal and distribution of the 71 sampling units in the high- and low-intensity farmland areas, with examples of landscape changes from 1995–1997 to 2010–2012.

4.3.3 Habitat characterization

We characterised the habitats within 250-m buffers (32.12 ha) of each transect using the land cover maps for 1995–1997 and 2010–2012 described in Santana *et al.* (2017a) (Fig. 4.1). Briefly, maps were produced using digital aerial photographs from 1995 (scale 1:40,000), and Bing Aerial images from October 2010 to July 2011, respectively. Mapping was refined with information from a governmental database of agricultural land uses at the parcel scale (Ribeiro *et al.* 2014), using data from 2000 and 2010 to represent crop types in 1995–1997 and 2010–2012, respectively. Using a single land cover map for each study period is reasonable because our land cover categories were not expected to drastically change within each 3-year period. These categories were selected to reflect potentially important bird habitats, considering both the natural (woodlands, open woodlands, shrublands, streams, and water bodies) and production (annual dry crops and fallows, permanent pastures, annual irrigated crops, arable land with scattered trees, and permanent crops) components of the landscape (Santana *et al.* 2017a). We also computed metrics reflecting habitat diversity and configuration

(number of different cover types, mean patch size, and edge density), which were estimated separately for the natural and the production components, using Fragstats 4.2 (McGarigal & Ene 2013).

4.3.4 Landscape heterogeneity

Landscape heterogeneity was estimated following the approach described by Anderson *et al.* (2006), which was previously used in our study area to compare landscape patterns across farming systems (Ribeiro *et al*. 2016a). First, we computed for each farmland area and time period the average dissimilarity in habitat characteristics from individual transects to their group centroid in multivariate space, which is a multivariate dispersion metric that can be interpreted as a measure of overall landscape heterogeneity (Anderson *et al.* 2006). To avoid inflating the effects of potentially correlated variables, estimates were made using the axes of a principal component analysis on the habitat variables (Habitat PCA) (see below). Second, we estimated dispersion along each independent Habitat PCA axis, to evaluate which habitat gradients contributed the most to overall landscape heterogeneity. Finally, we estimated pairwise landscape heterogeneity as the Euclidean distance between each pair of transects along each Habitat PCA (Anderson *et al.* 2006), which was used in analyses relating β-diversity metrics to landscape heterogeneity (see below).

4.3.5 Bird surveys

In each study year, transects were walked in early morning and late afternoon in April–May, and birds species detected within 250-m bands were registered (details in Santana *et al.* 2014). The months of sampling were adjusted to cover the breeding periods of both resident species and trans-Saharan migrants (Table S4.1). Before analysis, we pooled species occurrences at each transect within each 3-year period, to minimise potential confounding effects resulting from year-to-year fluctuations in species occurrences unrelated to local habitat conditions, differences in observer skills, and the possibility of missing some species when sampling on a single sampling occasion per year. To aid interpretation of ecological effects, bird species were categorised according to their specialization in farmland habitats (Santana *et al.* 2014; Table S4.1): farmland birds – species associated with a range of farmland habitats (e.g. arable fields, permanent crops, hedgerows); and steppe birds – a subset of farmland birds occurring only in open grassland habitats. We also categorised birds with unfavourable conservation status in Europe (SPEC1-3, BirdLife International 2004). Aquatic birds were discarded because they were not adequately sampled (Table S4.1). Because no birds were observed for some transects in a given period, they were discarded from subsequent analyses,

corresponding to three transects for steppe birds, and two transects for the other bird categories.

4.3.6 Bird diversity metrics

The γ-diversity in each farmland area was computed for each 3-year period, while correcting for differences in sampling effort between areas. We used Chao estimator implemented in 'iNEXT' (Hsieh *et al.* 2016) for R 3.2.3 (R Core Team 2016), assuming that sampling was thorough enough so that the landscape heterogeneity was well captured within the sampled sites (Santana *et al.* 2017a). Specifically, we estimated how many species would be observed if sample size was as large in high- as in low-intensity farmland, and computed the 95% confidence intervals of estimates. Sample-size-based rarefaction and sample completeness curves were used to evaluate whether our sampling effort was reasonable to estimate species richness.

Estimates of α-diversity were taken from Santana *et al*. (2017a), and they were used here to allow comparisons with spatial and temporal trends in β- and γ-diversity. Total beta diversity (β_{Tot}) was estimated by calculating pairwise dissimilarity in species composition between all pairs of transects within each farmland area and period, using the Jaccard index (Legendre 2014). The index was additively decomposed into two components to identify the dominant process driving compositional change: i) species replacement (β_{Repl}) – differences in species composition between transects; and ii) species richness difference ($\beta_{RichDiff}$) – differences in the number of species between transects (Legendre 2014; see Table S4.2 for formulation). The different number of transects sampled in each farmland area was unlikely to have effects on pairwise β-diversity metrics because they were based on the average of the differences in species composition between transects. The mean and the range of the distances between transects were similar in high- (mean distance between transects; min-max: 8.6km; 0.76–22.7km) and low-intensity farmland (10.4km; 0.79–23.0km).

4.3.7 Statistical analysis

Before analysis, we used the angular transformation on proportional data and the log-transformation on habitat diversity and configuration metrics, to minimize potential problems associated with the unit sum constraint and the undue influence of extreme values. For each farmland area, we then carried out a principal component analyses of habitat variables (Habitat PCA), with varimax rotation on components with eigenvalues >1.0 (Legendre & Legendre 1998), to describe the main habitat gradients and estimate landscape heterogeneity metrics. Land cover types with less than three occurrences were excluded to reduce the possible unduly large influence of rare land-

use categories (Legendre & Legendre 1998). We used t-tests to evaluate differences between time periods in the mean (habitat patterns) and dispersion (overall landscape heterogeneity) of transect scores along each Habitat PCA axis.

We used multiple linear models to analyse how β_{Tot}, β_{Repl}, and $\beta_{RichDiff}$ varied between time periods (1995-1997 [0] *versus* 2010-2012 [1]) and farmland area (high-intensity [0] *versus* low-intensity [1]), and whether temporal trends varied between farmland area (interaction term). Under our model parameterization, positive coefficients for the interaction term indicate that temporal trends in β-diversity metrics were more positive (or less negative) in low-intensity farmland compared to high-intensity farmland. The significance of model coefficients was tested using a permutation approach (Legendre & Legendre 1998), because the underlying data matrix was comprised of pairwise indices that are computed for all combinations of two transects, thereby inflating estimates of parametric significance due to pseudo-replication. Therefore, we compared the coefficients estimated for each model with the frequency distribution of coefficients estimated using 10,000 random permutations of transects among farmland areas, and time periods, but maintaining the original number of transects per area and period.

We used multiple regression on distance matrices (MRM; Lichstein 2007) to model the relationships between pairwise β-diversity metrics and pairwise landscape heterogeneity along each Habitat PCA axis. A separate model was fit for each farmland area and time period, including in each case all principal components and the matrix of geographical distances between the coordinates of transects to account for spatial autocorrelation (Lichstein 2007). We did not use any model selection procedure, because the number of variables was low in relation to the number of observations, and variables were not intercorrelated. Statistical significance of model coefficients was estimated using a permutation procedure with 10,000 permutations (Legendre *et al.* 1994).

To help explain the observed variations of β-diversity metrics in terms of actual spatial variations in bird assemblage composition (e.g. Legendre *et al.* 2005; Tuomisto & Ruokolainen 2006), we used partial constrained correspondence analysis (pCCA) (Legendre & Legendre 1998) to investigate how assemblage composition varied in relation to the gradients derived from the Habitat PCA. This analysis provides information on what species contribute to differences in assemblage composition between transects (i.e. β-diversity), and how such differences are driven by variation in habitat characteristics between transects (i.e. landscape heterogeneity) (Legendre *et al.* 2005; Tuomisto & Ruokolainen 2006). The pCCA was carried out separately for high- and low-intensity farmland, using the presences of the most widespread species, i.e. species with >25 % of occurrences in the dataset considering the two 3-year periods. We used the

habitat gradients obtained by PCA as constraining variables, and the sampling period as a conditioning variable. Model building was based on a forward-backward stepwise procedure, using Monte Carlo permutation tests with 10,000 permutations (Oksanen *et al.* 2016).

Analyses were performed in R 3.2.3 (R Core Team 2016), using 'psych' (Revelle 2015) and 'GPArotation' (Bernaards & Jennrich 2005) for PCA, 'lm' for multiple linear models, 'ecodist' (Goslee & Urban 2007) for MRM, and 'vegan' (Oksanen *et al*. 2016) for pCCA.

4.4 Results

4.4.1 Habitat patterns and landscape heterogeneity

In high-intensity farmland, the Habitat PCA extracted five axes (74.9% of variation; Tables S4.3), three of which showed significant variation between 1995–1997 and 2010–2012 in mean transect scores (Table 4.1), reflecting temporal habitat changes. Over time, there were increases in permanent crops and crop patch size, and declines in irrigated crops, crop richness and edge density ($PC2_{high}$; 21.5%); increases in pastures and water bodies ($PC4_{high}$; 10.3%); and increases in annual irrigated crops and declines in open fields with scattered trees, annual dry crops and fallows ($PC5_{high}$; 9.2%). No significant temporal changes were found along the gradient from predominantly agricultural habitats, with larger crop patches, to more natural habitats with higher cover by streams and woodlands, and higher natural habitat richness and edge density ($PC1_{high}$; 23.4%), nor along the gradient reflecting increases in open woodland cover and natural habitat patch size ($PC3_{high}$; 10.5%). Regarding landscape heterogeneity, the multivariate dispersion of transect scores did not change significantly over time, but dispersion increased significantly along $PC2_{high}$ and $PC4_{high}$ (Table 4.1).

In low-intensity farmland, mean transect scores varied significantly across time periods in two out of six axes extracted from the Habitat PCA (82.3% of variation; Tables 4.1, S4.4). In 2010–2012, there were increases in permanent pastures at the expense of annual dry crops and fallows ($PC3_{low}$; 11.8%), and increases in water bodies ($PC5_{low}$; 7.6%). No changes were found along the gradients reflecting increases in predominantly agricultural habitats, with larger crop patches, at the expense of natural habitats with higher cover by shrubland, streams and woodlands, more natural habitat types, and higher edge densities ($PC1_{low}$; 26.7%); increases in agricultural habitats at the expense of habitats with more open woodland and larger natural habitat patches ($PC2_{low}$; 18.1%); increases in arable land with scattered trees ($PC4_{low}$; 9.7%); and increases in annual irrigated crops ($PC6_{low}$; 8.4%). Overall landscape heterogeneity did

not change significantly over time, but heterogeneity increased significantly along $PC5_{low}$ and declined along $PC6_{low}$ (Table 4.1).

4.4.2 Bird diversity

The number of transects was always sufficient to record over 90% of species in each farmland area and period (Fig. S4.1). The estimated total number of species (γ-diversity) was much lower in high- than in low-intensity farmland in 1995–1997, but not in 2010–2012, when richness increased markedly in both areas (Fig. 4.2). A similar pattern was found for farmland and SPEC1-3 species groups, while the richness of steppe birds remained higher in low-intensity farmland in both periods, and variation between periods was much smaller (Fig. 4.2). Overall, variation in α-diversity was broadly similar to that of γ-diversity, albeit with a less pronounced increase between time periods, particularly in high-intensity farmland.

Table 4.1 **-** Temporal variation between 1995–1997 (T0) and 2010–2012(T1) in habitat patterns and landscape heterogeneity in the study area. Habitat change was estimated from paired *t*-tests comparing the mean scores of bird sampling transects along the axis extracted from principal component analysis of habitat variables (PC#), in high- and low-intensity farmland (Tables S4.3 and S4.4). Landscape heterogeneity was estimated from paired *t*-tests comparing the dispersion of scores, either along each axis (PC#) or in multivariate space (All PC). Bold denotes $P < 0.05$

Habitat gradient	**Habitat patterns**				**Landscape heterogeneity**			
	T0	**T1**	***t***	***P***	**T0**	**T1**	***t***	***P***
High-intensity farmland (n=28)								
$PC1_{high}$ (Agricultural to natural habitats)	-0.12	0.12	1.98	0.058	0.87	0.72	-0.94	0.353
$PC2_{high}$ (Annual irrigated to permanent crops)	**-0.38**	**0.38**	**3.75**	**0.001**	**0.42**	**0.99**	**4.06**	**<0.001**
$PC3_{high}$ (Open woodlands and natural habitat patches)	0.13	-0.13	-1.32	0.197	0.60	0.63	0.13	0.894
$PC4_{high}$ (Permanent pastures and water bodies)	**-0.36**	**0.36**	**2.91**	**0.007**	**0.35**	**0.81**	**2.46**	**0.018**
$PC5_{high}$ (Annual irrigated crops to arable land with scattered trees)	**0.27**	**-0.27**	**-3.16**	**0.004**	0.80	0.57	-1.24	0.220
All PC $_{high}$					1.94	2.02	0.37	0.711
Low-intensity farmland (n=43)								
$PC1_{low}$ (Agricultural to natural habitats)	0.01	-0.01	-0.22	0.830	0.81	0.79	-0.17	0.864
$PC2_{low}$ (Agricultural habitats to open woodlands)	-0.02	0.02	0.88	0.384	0.74	0.70	-0.23	0.818
$PC3_{low}$ (Permanent pastures to annual dry crops and fallows)	**0.40**	**-0.40**	**-4.89**	**<0.001**	0.77	0.68	-0.69	0.491
$PC4_{low}$ (Arable land with scattered trees)	-0.01	0.01	0.20	0.846	0.67	0.62	-0.25	0.799
$PC5_{low}$ (Water bodies)	**-0.20**	**0.20**	**2.92**	**0.006**	**0.51**	**0.94**	**3.18**	**0.002**
$PC6_{low}$ (Annual irrigated crops)	0.17	-0.17	-1.67	0.102	**0.79**	**0.34**	**-2.67**	**0.011**
All PC $_{low}$					2.15	2.20	0.27	0.790

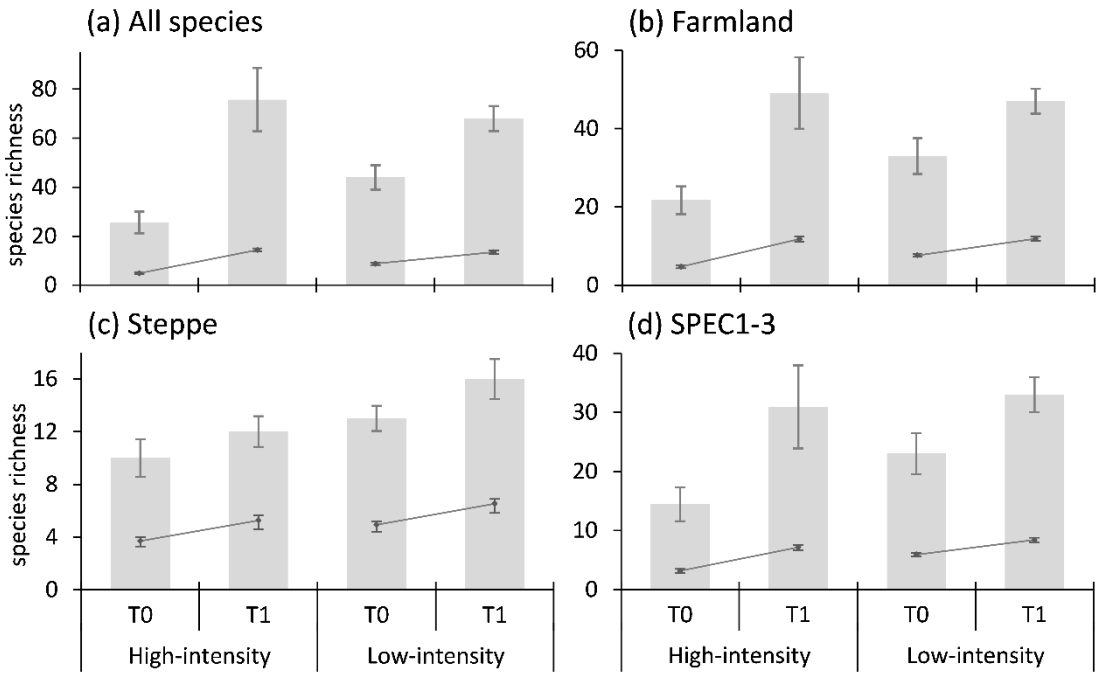

Fig. 4.2 - Estimates of α-diversity (dots) and γ-diversity (bars) of the total (a), farmland (b), steppe (c) and species of European conservation concern (SPEC1-3; d) bird assemblages, in high- and low-intensity farmland, before (1995–1997) and after (2010–2012) the CAP reform of 2003. We estimated α-diversity as the mean (± standard error) species richness per transect, and γ-diversity (± 95% confidence intervals) using Chao's estimator (Fig. S4.1).

Variation in β_{Tot} was significantly affected by farmland area, sampling period, and their interaction (Table 4.2). In general, β_{Tot} was much higher in low- than in high-intensity farmland in 1995–1997, but the two converged to much the same values in 2010–2012, mainly due to a sharp increase in high-intensity, and a small decline in low-intensity farmland (Fig. 4.3). Similar results were found for β_{Repl} of total, farmland and SPEC1-3 species (Fig. 4.3, Table 4.2), with sharp increases in high-intensity farmland and stability or slight declines in low-intensity farmland (Fig. 4.3). This pattern was broadly similar but not statistically significant for steppe birds (Fig. 4.3, Table 4.2). There were declines between time periods for $\beta_{RichDiff}$ of total, farmland and SPEC1-3 species, while $\beta_{RichDiff}$ of SPEC1-3 species was higher in high- than in low-intensity farmland (Table 4.2; Fig. 4.3). There were no interaction effects for $\beta_{RichDiff}$.

4.4.3 Effects of landscape heterogeneity on beta diversity

In high-intensity farmland, there were only a few significant relations between β-diversity and landscape heterogeneity (Table S4.5). In 1995–1997, $\beta_{RichDiff}$ and β_{Repl} of the total assemblage were positively and negatively related, respectively, to heterogeneity along $PC5_{high}$ (annual irrigated crops versus arable land with scattered trees). In 2010–2012, β_{Repl} of the total and farmland bird assemblages were positively related to heterogeneity along $PC2_{high}$ (annual irrigated versus permanent crops).

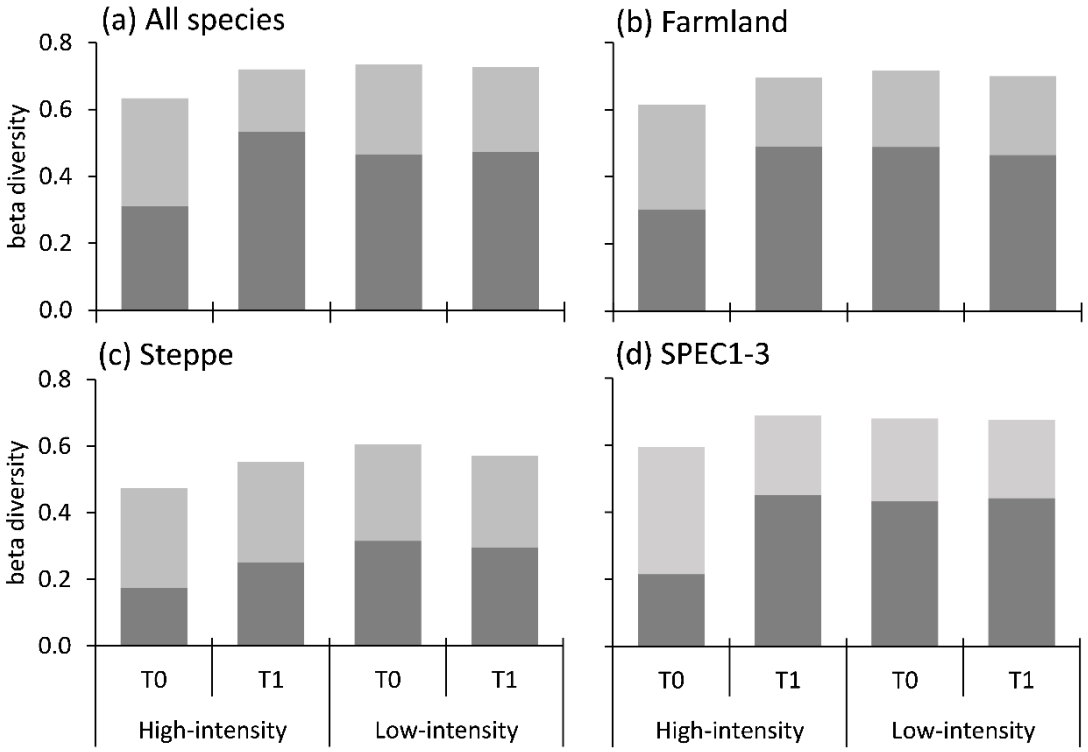

Fig. 4.3 - Estimates of total beta diversity, and its species replacement (dark grey) and richness difference (light grey) components, for the total (a), farmland (b), steppe (c) and species of European conservation concern (SPEC1-3; d) bird assemblages, in high- and low-intensity farmland, before (1995–1997) and after (2010–2012) the CAP reform of 2003.

In low-intensity farmland, there were several significant relations between β-diversity and landscape heterogeneity (Table S4.6). There were often significant positive relations between β_{Tot}, β_{Repl} (mainly in 1995–1997), and $\beta_{RichDiff}$ (mainly in 2010–2012) and the geographical distance between transects. In both periods, β_{Tot} and β_{Repl} were often positively related to heterogeneity along $PC1_{low}$ (more agricultural versus more natural habitats) and $PC2_{low}$ (more agricultural habitats versus open woodland) gradients, while relations for $\beta_{RichDiff}$ tended to be negative. In 2010–2012, β_{Repl} and $\beta_{RichDiff}$ of steppe birds were negatively and positively related, respectively, to heterogeneity along $PC4_{low}$ (increasing cover by arable land with scattered trees).

4.4.4 Bird assemblage variation in relation to landscape heterogeneity

In high-intensity farmland, the first pCCA (41.4% of variance) reflected a progressive replacement of steppe (little bustard) and some generalist farmland (quail *Coturnix coturnix*, zitting cisticola *Cisticola juncidis,* red-legged partridge *Alectoris rufa*, and bee-eater *Merops apiaster*) species, by other generalist farmland (sparrows *Passer* spp., goldfinch *Carduelis carduelis,* and barn swallow *Hirundo rustica*) and non-farmland (stonechat *Saxicola rubicola*, blackbird *Turdus merula*) species, and was significantly associated with gradients from more agricultural to more natural habitats ($PC1_{high}$, *F*=

3.56, *P*<0.001), and of increasing cover by permanent versus annual irrigated crops ($PC2_{high}$, *F*=3.31, *P*<0.001) (Fig. 4.4a). The second pCCA (31.4%) reflected a replacement between species associated with either increasing cover by permanent crops ($PC2_{high}$; bee-eater, greenfinch *Chloris chloris*, black-eared wheatear *Oenanthe hispanica*, and blackbird), or with more natural habitats ($PC1_{high}$) and arable land with scattered trees ($PC5_{high}$, *F*=1.83, *P*=0.042), such as red-legged partridge, zitting cisticola, barn swallow, stonechat, and sparrows.

Table 4.2 - Models relating bird total beta diversity (β_{tot}), species replacement (β_{Repl}), and species richness differences ($\beta_{RichDiff}$), to time period (1995–1997 [0] vs. 2010–2012 [1]) and farmland area (high-intensity [0] vs. low-intensity [1]). For each model we present the estimated coefficients (Coef) and standard error (SE), and their statistical significance for two-tailed tests (*P*). Significant differences (*P* < 0.05) are in bold and negative coefficients are underlined. A positive interaction coefficient implies that diversity metrics increased more in low- than in high-intensity farmland; negative coefficients indicate the opposite trend

Beta diversity metric	Time period			Farmland Area			Period × Area		
	Coef	SE	*P*	Coef	SE	*P*	Coef	SE	*P*
All species									
β_{tot}	**0.09**	**0.01**	**0.001**	**0.10**	**0.01**	**<0.001**	**-0.10**	**0.01**	**0.004**
β_{Repl}	**0.22**	**0.01**	**<0.001**	**0.15**	**0.01**	**0.003**	**-0.21**	**0.02**	**0.003**
$\beta_{RichDiff}$	**-0.14**	**0.01**	**0.011**	-0.05	0.01	0.287	0.12	0.02	0.085
Farmland									
β_{tot}	**0.08**	**0.01**	**0.001**	**0.10**	**0.01**	**<0.001**	**-0.10**	**0.01**	**0.002**
β_{Repl}	**0.19**	**0.01**	**<0.001**	**0.19**	**0.01**	**<0.001**	**-0.21**	**0.02**	**0.003**
$\beta_{RichDiff}$	**-0.11**	**0.01**	**0.038**	-0.08	0.01	0.063	0.11	0.02	0.086
Steppe									
β_{tot}	**0.08**	**0.01**	**0.038**	**0.13**	**0.01**	**<0.001**	**-0.11**	**0.02**	**0.018**
β_{Repl}	0.08	0.02	0.164	**0.14**	**0.01**	**0.004**	-0.09	0.02	0.170
$\beta_{RichDiff}$	0.00	0.02	0.931	-0.01	0.01	0.866	-0.02	0.02	0.759
SPEC 1-3									
β_{tot}	**0.09**	**0.01**	**<0.001**	**0.09**	**0.01**	**0.001**	**-0.10**	**0.01**	**0.003**
β_{Repl}	**0.24**	**0.02**	**<0.001**	**0.22**	**0.01**	**<0.001**	**-0.23**	**0.02**	**0.006**
$\beta_{RichDiff}$	**-0.14**	**0.01**	**0.023**	**-0.13**	**0.01**	**0.020**	0.13	0.02	0.110

In low-intensity farmland, the first pCCA (62.2%) reflected the replacement of steppe bird species of conservation concern such as great bustard, little bustard, calandra lark *Melanocorypha calandra*, and short-toed lark, by more generalist farmland species of lower concern such as bee-eater, *Galerida* larks, barn swallow, and red legged-partridge, and was significantly associated with gradients from more agricultural habitats to either more natural habitats ($PC1_{low}$, *F*=5.59, *P*<0.001) or habitats with higher cover by open woodlands and large natural patches versus agricultural habitats ($PC2_{low}$, *F*=5.72, *P*=<0.001) (Fig. 4.4b). The second pCCA (15.6%) was mainly related to increasing cover by arable land with scattered trees ($PC4_{low}$, *F*=3.97, *P*=<0.001) and, to

a lesser extent, to the agricultural-natural gradient ($PC1_{low}$), which was associated with the replacement of species such as white stork, great bustard and calandra lark, by species such as Montagu's harrier *Circus pygargus*, red-legged partridge and little bustard.

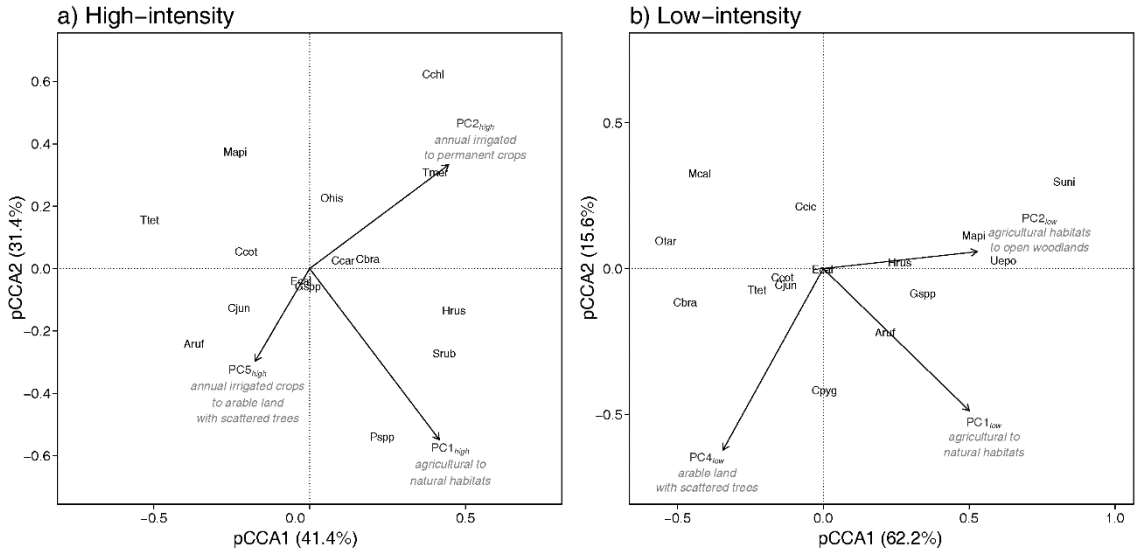

Fig. 4.4 - Biplot of the first two axes extracted from a partial canonical correspondence analysis (pCCA) in the high- (a) and low-intensity (b) farmland areas, showing the influence of landscape heterogeneity described by the main habitat gradients (arrows) on variation in bird assemblage composition (β-diversity). The proportion of total variation represented in each axis is also provided. Species abbreviations are provided in Table S4.1.

4.5 Discussion

Our study supported the idea that the expansion of previously scarce land uses after the CAP reform of 2003 contributed to increasing landscape heterogeneity, mainly due to spreading out of permanent crops (i.e. olive groves) in high-intensity farmland (Ribeiro *et al.* 2014). Also, we found that α-diversity was the main driver of the temporal increase in γ-diversity in low-intensity farmland, while both α- and β-diversity (β_{Repl}, but not $\beta_{RichDiff}$) strongly contributed to increase γ-diversity in high-intensity farmland. These patterns were largely similar for all species groups, albeit much less markedly for steppe birds. There were significant relationships between β-diversity and landscape heterogeneity, but the actual land-use types influencing such relationships varied between areas, time periods, and species group considered. Finally, we found that β-diversity was associated with the spatial replacement of species with contrasting habitat affinities along the main gradients of environmental heterogeneity, involving in some cases the replacement of steppe birds of high conservation concern by more common and generalist species. Overall, our study supports the value of β-diversity in conservation research (Socolar *et al.* 2016), by showing that information on patterns and drivers of spatial variation in

assemblage composition add significantly to the analysis of local species richness for providing meaningful conservation management prescriptions on farmland.

Before the CAP reform (1995–1997), the higher bird diversity observed in low- than in high-intensity farmland was probably a consequence of its more favourable agricultural habitats and landscape heterogeneity patterns. During this period, the low-intensity area was dominated by a traditional farming system (Ribeiro *et al.* 2014), with high α-diversity likely supported by the presence of favourable habitats such as woodlands, riparian vegetation and fallows (Delgado & Moreira 2000; Stoate *et al.* 2003; Santana *et al.* 2017a), and probably also by beneficial crop management practices (Ribeiro *et al.* 2016b). Likewise, our results suggest that high β-diversity was supported by high landscape heterogeneity, particularly with that associated with the gradient from natural to agricultural habitats. This gradient strongly affected spatial variation in assemblage composition, primarily through species replacement (β_{Repl}). The favourable conditions for both α- and β-diversity thus probably contributed to the relatively high γ-diversity estimated in low-intensity farmland.

In marked contrast, the low diversity observed in high-intensity farmland in 1995–1997 probably resulted from the prevalence of a farming system specialised on annual irrigated crops (Ribeiro *et al.* 2014), which was likely associated with poor bird habitats and landscape homogeneity (Ribeiro *et al.* 2016a,b). These crops tend to support low α-diversity in Mediterranean farmlands, probably due to their structural characteristics, the heavy use of agro-chemicals and other unfavourable management practices (Stoate, Araújo & Borralho 2003; Brotons *et al.* 2004; Santana *et al.* 2017a). The production of annual irrigated crops is also associated with low landscape heterogeneity (Ribeiro *et al.* 2016b), which probably explains the low β-diversity in high-intensity farmland, and the lack of consistent relations between β-diversity and landscape heterogeneity observed in this area. Although we found a tendency similar to that of low-intensity farmland for assemblage composition changing along the gradient from natural to agricultural habitats, this was probably not sufficient to increase the overall β-diversity due to the low representation of natural habitats in high-intensity farmland (Santana *et al.* 2017a). Whatever the mechanism, these low values of both α- and β-diversity were responsible for the low γ-diversity observed in high-intensity farmland before the CAP reform of 2003.

After the CAP reform (2010–2012), diversity metrics (except $\beta_{RichDiff}$) largely increased and converged in high-intensity farmland to the values observed in low-intensity farmland. It is unlikely that these changes were primarily due to biases arising from variations in species detectability, because the open habitats with high visibility were largely retained across sampling periods in low-intensity farmland, while the number of species detected in high-intensity farmland increased markedly despite the

expansion of closed habitats with potentially lower visibility (i.e. permanent crops). It is more likely that the increase in α-diversity observed in low-intensity farmland reflected a positive effect of conservation management of the SPA, without any noticeable negative effects of the transition from traditional to livestock specialised farming systems (Santana *et al.* 2014; Ribeiro *et al.* 2014). This farming system change did not affect the main gradients of landscape heterogeneity (Ribeiro *et al.* 2016b; this study), which probably explains the lack of change in β-diversity observed in this farmland area. Regarding high-intensity farmland, the increase in α-diversity was probably due to the expansion of olive groves at the expense of annual irrigated crops, providing habitat for a range of woodland and shrubland species that were previously absent or scarce in this area (Santana *et al.* 2014, 2017a). This change also contributed to increased landscape heterogeneity, which was likely responsible for the observed increase in β-diversity, mainly due to species replacement (β_{Repl}) among sites dominated by contrasting agricultural habitats. In fact, the gradient from annual irrigated crops to olive groves was strongly associated with spatial variation in assemblage composition, thereby promoting the coexistence of more species. Overall, therefore, while the increase in γ-diversity observed in low-intensity farmland was mainly driven by increasing α-diversity, both α- and β-diversity were responsible for the increase in γ-diversity in high-intensity farmland.

4.6 Conservation implications

This study illustrates how β-diversity can be used to provide practical insights on the management of specific farmland areas, beyond those supported solely on information from the local patterns of assemblage richness and composition (e.g. Delgado & Moreira 2000; Stoate *et al.* 2003; Santana *et al.* 2014, 2017a). In our low-intensity farmland area, results suggest that management should be directed at maintaining a stable β-diversity, with any temporal increases in β-diversity potentially reflecting negative conservation outcomes. This is because the area is devoted to steppe bird conservation, and high β-diversity was associated with the spatial replacement of steppe bird species by species of low conservation concern. Therefore, maintaining the dominance of open agricultural habitats is critical in this and possibly other farmland areas (e.g. Báldi & Bátáry 2011), even though this may be negative for landscape heterogeneity, and for overall β- and γ-diversity. In contrast, managing for high β-diversity may be sensible in our high-intensity farmland area, where increases in β-diversity after the CAP reform of 2003 probably reflect positive conservation outcomes. This is because increasing overall diversity rather than the diversity of any particular species group is generally the main goal in high-intensity farmland (e.g. Fahrig *et al.* 2011; Karp et al. 2012), and in our case this was

favoured by recent increases in landscape heterogeneity associated with the expansion of olive groves. Therefore, maintaining a patchwork of arable and permanent crops may be a key management goal in this area, as this provides conditions for both farmland and woodland and shrubland species at the landscape scale (Santana *et al*. 2017a), and thus high β- and γ-diversity. Further expansion of olive groves may turn out to be negative, however, if it leads to progressive homogenization of the landscape, requiring this potential outcome to be assessed through continued monitoring of β-diversity.

In general, our study underlined the value of β-diversity to inform agricultural policies and conservation actions on farmland, supporting previous suggestions that it may be essential to capture processes that are hard or impossible to detect using only local diversity metrics (Clough *et al.* 2007; Gaston *et al.* 2007; Monnet *et al.* 2014; Socolar *et al.* 2016; Żmihorski *et al.* 2016). First, our results illustrated the importance of β-diversity to understand the consequences of land-use changes, as focusing solely on α-diversity would have missed important links between biodiversity and anthropogenic drivers. This was particularly evident in high-intensity farmland, where variation in γ-diversity was mainly driven by β-diversity. Second, the analysis of β-diversity helped identify the main land-use types shaping functional landscape heterogeneity (sensu Fahrig *et al.* 2011), which is critical for farmland conservation management. In fact, although there was a variety of land uses shaping a range of habitat gradients, only heterogeneity associated with the gradients from agricultural to natural habitats in the low-intensity farmland area, and from arable to permanent crops in the high-intensity farmland area, could be considered functional, in the sense that they strongly affected spatial variation in assemblage composition. Finally, our results showed that while temporal variations in β-diversity may be used to assess biodiversity trends, the meaning of such changes should be carefully considered, as we found high levels of β-diversity to be linked with potentially negative conservation outcomes in low-intensity farmland. This supports the view that higher β-diversity does not necessarily equate to higher conservation value (Socolar *et al.* 2016), and thus that the management of landscape heterogeneity and β-diversity should be fine-tuned in relation to well-defined conservation goals (e.g. Báldi & Batáry 2011).

4.7 Authors' Contributions

JS and PB conceived the study; JS produced land cover maps with help of LR, PB, PFR and FM; JS analysed the data with the assistance of MP, PB and JTR; JS wrote the first draft of the manuscript with the assistance of PB and JTR; LR collected part of bird data

and prepared bird data database with help of JS; all authors read and commented on drafts of the manuscript.

4.8 Acknowledgements

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4.9 Data accessibility

Bird and habitat data used in this study are available through the Dryad Digital Repository, http://dx.doi.org/10.5061/dryad.kp3fv (Santana *et al*. 2017b).

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4.11 Supporting information

Table S4.1 - List of bird species recorded in high- and low-intensity farmland areas in southern Portugal, before (1995-1997) and after (2010-2012) the CAP reform of 2003. For each species we provide the habitat affinities (Habitat), European conservation status (Status), phenology, and percentage of transects where the species was recorded.

Species[1]	Abbr	Habitat[2]	Status[3]	Phenology	High-intensity (n=28)		Low-intensity (n=43)	
					1995-1997	2010-2012	1995-1997	2010-2012
Galliformes								
Alectoris rufa	Aruf	Farmland	SPEC 2	Resident	7.1	42.9	23.3	48.8
Coturnix coturnix	Ccot	Farmland (Steppe)	SPEC 3	Migrant	67.9	60.7	48.8	46.5
Ciconiiformes								
Bubulcus ibis		Farmland		Resident	3.6	3.6	25.6	16.3
Ciconia nigra		Non-farmland	SPEC 2	Migrant	0	0	2.3	0
Ciconia ciconia	Ccic	Farmland	SPEC 2	Resident/Migrant	0	14.3	25.6	46.5
Accipitriformes								
Elanus caeruleus		Farmland	SPEC 3	Resident	0	10.7	2.3	4.7
Milvus migrans		Farmland	SPEC 3	Migrant	0	10.7	7.0	7.0
Milvus milvus		Farmland	SPEC 2	Migrant	0	3.6	0	2.3
Gyps fulvus		Farmland		Resident	0	0	0	2.3
Circaetus gallicus		Non-farmland	SPEC 3	Migrant	0	3.6	0	4.7
Circus aeruginosus		Non-farmland		Migrant	0	3.6	0	2.3
Circus pygargus	Cpyg	Farmland (Steppe)		Migrant	7.1	14.3	34.9	41.9
Buteo buteo		Farmland		Resident	0	14.3	2.3	11.6
Aquila adalberti		Non-farmland	SPEC 1	Resident	0	0	0	7.0
Aquila pennata		Non-farmland	SPEC 3	Migrant	0	3.6	0	0
Aquila fasciata		Farmland	SPEC 3	Resident	0	0	0	4.7
Falconiformes								
Falco naumanni		Farmland (Steppe)	SPEC 1	Migrant	0	0	2.3	46.5
Falco tinnunculus		Farmland	SPEC 3	Resident	0	14.3	2.3	7.0
Gruiformes								

Species[1]	Abbr	Habitat[2]	Status[3]	Phenology	High-intensity (n=28)		Low-intensity (n=43)	
					1995-1997	2010-2012	1995-1997	2010-2012
Tetrax tetrax	Ttet	Farmland (Steppe)	SPEC 1	Resident	42.9	32.1	65.1	74.4
Otis tarda	Otar	Farmland (Steppe)	SPEC 1	Resident	0	10.7	32.6	32.6
Charadriiformes								
Burhinus oedicnemus		Farmland (Steppe)	SPEC 3	Resident	7.1	25.0	9.3	20.9
Glareola pratincola		Farmland (Steppe)	SPEC 3	Migrant	0	0	0	2.3
Pteroclidiformes								
Pterocles orientalis		Farmland (Steppe)	SPEC 2	Resident	0	0	0	20.9
Columbiformes								
Columba livia		Farmland		Resident	0	3.6	0	2.3
Columba palumbus		Non-farmland		Resident	0	14.3	0	9.3
Streptopelia decaocto		Farmland		Resident	0	28.6	0	18.6
Streptopelia turtur		Farmland	SPEC 3	Migrant	0	3.6	0	0
Cuculiformes								
Clamator glandarius		Farmland		Migrant	0	3.6	2.3	11.6
Cuculus canorus		Farmland		Migrant	0	0	9.3	11.6
Strigiformes								
Athene noctua		Farmland	SPEC 3	Resident	3.6	3.6	7.0	7.0
Coraciiformes								
Merops apiaster	Mapi	Farmland	SPEC 3	Migrant	3.6	50.0	18.6	55.8
Coracias garrulus		Farmland (Steppe)	SPEC 2	Migrant	0	3.6	0	4.7
Upupa epops	Uepo	Farmland	SPEC 3	Migrant	10.7	28.6	34.9	25.6
Piciformes								
Dendrocopos major		Non-farmland		Resident	0	0	0	2.3
Passeriformes								
Melanocorypha calandra	Mcal	Farmland (Steppe)	SPEC 3	Resident	0	0	51.2	62.8
Calandrella brachydactyla	Cbra	Farmland (Steppe)	SPEC 3	Migrant	17.9	42.9	53.5	25.6
Galerida spp.[4]	Gspp	Farmland (Steppe)	SPEC 3	Resident	14.3	85.7	27.9	69.8
Lullula arborea		Non-farmland	SPEC 2	Resident	0	10.7	18.6	9.3

Species[1]	Abbr	Habitat[2]	Status[3]	Phenology	High-intensity (n=28)		Low-intensity (n=43)	
					1995-1997	2010-2012	1995-1997	2010-2012
Hirundo rustica	Hrus	Farmland	SPEC 3	Migrant	14.3	42.9	23.3	46.5
Cecropis daurica		Farmland		Migrant	0	3.6	0	4.7
Delichon urbicum		Farmland	SPEC 3	Migrant	0	0	0	9.3
Anthus campestris		Farmland (Steppe)	SPEC 3	Migrant	7.1	28.6	2.3	14.0
Motacilla flava		Farmland		Migrant	0	3.6	0	4.7
Motacilla alba		Farmland		Resident	0	3.6	2.3	0
Cercotrichas galactotes		Non-farmland	SPEC 3	Migrant	0	0	0	2.3
Luscinia megarhynchos		Non-farmland		Migrant	3.6	28.6	4.7	7.0
Saxicola rubicola	Srub	Farmland		Resident	25.0	42.9	16.3	30.2
Oenanthe hispanica	Ohis	Farmland (Steppe)	SPEC 2	Migrant	17.9	39.3	11.6	11.6
Turdus merula	Tmer	Non-farmland		Resident	0	64.3	14.0	14.0
Turdus viscivorus		Non-farmland		Resident	0	3.6	0	0
Cettia cetti		Non-farmland		Resident	10.7	10.7	0	0
Cisticola juncidis	Cjun	Farmland (Steppe)		Resident	89.3	75.0	53.5	83.7
Acrocephalus scirpaceus		Non-farmland		Migrant	0	0	0	2.3
Acrocephalus arundinaceus		Non-farmland		Migrant	0	3.6	0	0
Hippolais polyglotta		Non-farmland		Migrant	0	7.1	0	0
Sylvia atricapilla		Non-farmland		Resident	0	3.6	0	0
Sylvia hortensis		Farmland	SPEC 3	Migrant	0	3.6	0	0
Sylvia undata		Non-farmland	SPEC 2	Resident	0	0	0	4.7
Sylvia cantillans		Non-farmland		Migrant	0	3.6	0	2.3
Sylvia melanocephala		Non-farmland		Resident	0	17.9	20.9	14.0
Phylloscopus collybita		Non-farmland		Migrant	0	3.6	0	0
Phylloscopus ibericus		Non-farmland		Migrant	0	3.6	0	0
Aegithalos caudatus		Non-farmland		Resident	0	0	2.3	0
Cyanistes caeruleus		Non-farmland		Resident	0	7.1	14	18.6
Parus major		Non-farmland		Resident	3.6	3.6	18.6	16.3
Certhia brachydactyla		Non-farmland		Resident	0	10.7	4.7	7.0

Species[1]	Abbr	Habitat[2]	Status[3]	Phenology	High-intensity (n=28)		Low-intensity (n=43)	
					1995-1997	2010-2012	1995-1997	2010-2012
Oriolus oriolus		Non-farmland		Migrant	0	0	0	2.3
Lanius meridionalis		Farmland		Resident	10.7	28.6	14	16.3
Lanius senator		Farmland	SPEC 2	Migrant	7.1	3.6	20.9	11.6
Garrulus glandarius		Non-farmland		Resident	0	0	0	7
Cyanopica cyanus		Non-farmland		Resident	0	39.3	0	11.6
Pica pica		Farmland		Resident	0	21.4	0	0
Corvus monedula		Farmland		Resident	0	0	0	4.7
Corvus corone		Farmland		Resident	0	46.4	0	11.6
Corvus corax		Non-farmland		Resident	0	0	7.0	7.0
Sturnus unicolor	Suni	Farmland		Resident	0	17.9	16.3	37.2
Passer spp.[5]	Pspp	Farmland		Resident	10.7	50.0	7	25.6
Fringila coelebs		Non-farmland		Resident	0	0	4.7	2.3
Serinus serinus		Farmland		Resident	0	10.7	0	0
Chloris chloris	Cchl	Farmland		Resident	10.7	39.3	0	9.3
Carduelis carduelis	Ccar	Farmland		Resident	0	75.0	9.3	34.9
Carduelis cannabina		Farmland	SPEC 2	Resident	0	46.4	0	7.0
Estrilda astrild		Non-farmland		Resident	0	3.6	0	0
Emberiza calandra	Ecal	Farmland (Steppe)	SPEC 2	Resident	92.9	89.3	100	95.3

[1] Species are listed in taxonomic order following Equipa Atlas (2008). The aquatic birds recorded are not listed because they were excluded from analysis: *Anas platyrhynchos, Anas strepera, Ardea cinerea, Casmerodius albus, Charadrius dubius, Egretta garzetta, Fulica atra, Gallinula chloropus, Himantopus himantopus, Larus michahellis, Platalea leucorodia, Sterna nilotica, Tachybaptus ruficollis,* and *Tringa ochropus.*

[2] Bird habitat categorizations based on Ehrlich *et al.* (1994), Equipa Atlas (2008), Reino *et al.* (2009), EBCC (2012), Suárez *et al.* (1997), and Reino *et al.* (2009).

[3] Species of European Conservation Concern: SPEC 1 - Species of global conservation concern; SPEC 2 - species concentrated in Europe and with an unfavorable conservation status; SPEC 3 - species not concentrated in Europe but with an unfavorable conservation status (BirdLife International 2004).

[4] *Galerida* spp.: includes *Galerida theklae*, *G. cristata* and *Galerida* sp. observations.

[5] *Passer* spp.: includes *Passer domesticus*, *P. hispaniolensis* and *Passer* sp. observations. We have not considered *Passe*r ssp. as a SPEC species because most of the identified records were from *P. hispaniolensis*.

Table S4.2 - Formulation of the indices used to estimate beta diversity and its components following Podani & Schmera (2011), Carvalho *et al.* (2012) and Carvalho *et al.* (2013). Pairwise dissimilarity index was used to calculate total community variation (β_{Tot}), which was additively partitioned into species replacement (β_{Repl}) and species richness difference ($\beta_{RichDiff}$), expressed as $\beta_{Tot} = \beta_{Repl} + \beta_{RichDiff}$.

Beta diversity metric	**Index***	**Description**
Pairwise dissimilarity (β_{Tot})	$\frac{(b + c)}{(a + b + c)}$	Overall compositional differences between sites
Species replacement (β_{Repl})	$\frac{2 \times \min(b, c)}{(a + b + c)}$	Differences in species composition between sites
Species richness difference ($\beta_{RichDiff}$)	$\frac{\lvert b - c \rvert}{(a + b + c)}$	Differences in the number of species between sites

*: *a* is the number of species present at both sites, and *b* and *c* are the number of species present only in one of the sites.

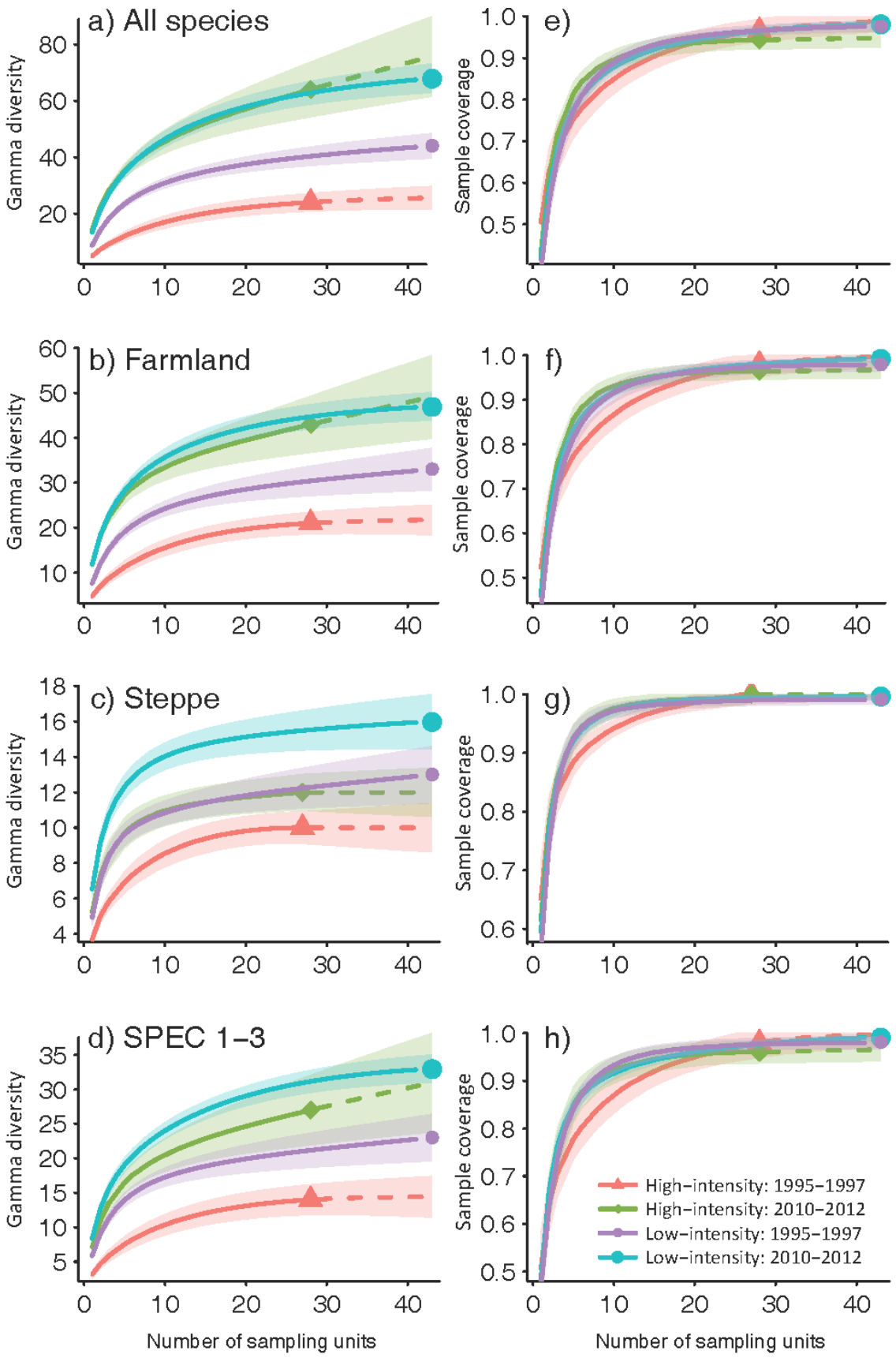

Fig. S4.1 - Sample-size-based rarefaction (solid lines) and extrapolation (dotted lines) curves (a-d), and sample completeness curves (e-h) in each farmland area and sampling period using Chao's estimator and q=0 (species richness). Shaded areas represent 95% confidence intervals of estimates. Separate panels are presented for the total bird assemblage (a,e), and for the farmland (b-f), steppe (c,g) and SPEC1-3 (d,h) groups of species.

Table S4.3 - Loadings of habitat variables in **high-intensity farmland** on varimax rotated axes (PC#$_{high}$) extracted from a principal component analysis (PCA). The eigenvalues and proportion of variation represented are provided for each PC. Values in bold indicate |factor loadings| > 0.5.

Variable (unit)	**PC1$_{high}$**[1]	**PC2$_{high}$**[2]	**PC3$_{high}$**[3]	**PC4$_{high}$**[4]	**PC5$_{high}$**[5]
Edge density of natural habitats (m^2/ha)	**0.90**	-0.27	0.20	0.08	0.04
Natural habitats richness (no)	**0.87**	-0.23	0.17	0.09	-0.01
Streams (% cover)	**0.78**	-0.09	0.02	-0.02	0.00
Woodland (% cover)	**0.54**	-0.11	-0.55	-0.15	0.19
Mean patch area of natural habitats (ha)	**0.54**	-0.09	**0.64**	0.33	-0.03
Edge density of crop (m^2/ha)	0.48	**-0.74**	0.09	0.19	0.20
Water bodies (% cover)	0.28	0.06	0.14	**0.63**	-0.01
Open woodland (% cover)	0.24	-0.12	**0.81**	-0.12	0.05
Arable land with scattered trees (% cover)	0.17	-0.24	-0.13	-0.02	**0.75**
Annual irrigated crops (% cover)	0.16	**-0.61**	-0.11	-0.36	**-0.61**
Crop richness (no)	0.16	**-0.84**	-0.06	0.11	-0.02
Permanent crops (% cover)	-0.07	**0.81**	-0.15	0.17	-0.24
Permanent pastures (% cover)	-0.12	-0.11	-0.08	**0.81**	-0.02
Annual dry crops and fallows (% cover)	-0.15	-0.48	0.21	-0.32	**0.53**
Mean patch area of crops (ha)	**-0.51**	**0.69**	-0.08	-0.18	-0.15
Eigenvalue	*3.50*	*3.23*	*1.57*	*1.55*	*1.37*
Percentage of variance (%)	*23.4*	*21.5*	*10.5*	*10.3*	*9.2*

[1] Agricultural to natural habitats.

[2] Annual irrigated to permanent crops.

[3] Open woodlands and natural habitat patches.

[4] Permanent pastures and water bodies.

[5] Annual irrigated crops to arable land with scattered trees.

Table S4.4 - Loadings of habitat variables in **low-intensity farmland** on varimax rotated axes (PC#$_{low}$) extracted from a principal component analysis (PCA). The eigenvalues and proportion of variation represented are provided for each PC. Values in bold indicate |factor loadings| > 0.5.

Variable (unit)	**PC1$_{low}$[1]**	**PC2$_{low}$[2]**	**PC3$_{low}$[3]**	**PC4$_{low}$[4]**	**PC5$_{low}$[5]**	**PC6$_{low}$[6]**
Edge density of natural habitats (m^2/ha)	**0.89**	0.26	0.03	-0.06	0.09	-0.06
Shrubland (% cover)	**0.85**	-0.15	0.11	0.06	-0.03	-0.03
Edge density of crop (m^2/ha)	**0.84**	0.01	-0.17	0.18	-0.01	0.11
Natural habitats richness (no)	**0.81**	0.31	-0.04	-0.01	0.29	0.00
Streams (% cover)	**0.60**	0.17	-0.04	-0.41	-0.27	-0.01
Woodland (% cover)	**0.51**	0.47	-0.09	-0.19	0.00	0.15
Open woodland (% cover)	0.21	**0.92**	0.02	-0.04	0.08	-0.08
Crop richness (no)	0.10	-0.13	-0.04	**0.69**	-0.20	0.53
Water bodies (% cover)	0.06	0.03	-0.03	0.05	**0.94**	0.07
Annual irrigated crops (% cover)	0.02	0.01	0.11	-0.06	0.12	**0.92**
Arable land with scattered trees (% cover)	0.01	0.09	0.04	**0.85**	0.11	-0.16
Mean patch area of natural habitats (ha)	-0.01	**0.90**	0.06	0.05	0.00	-0.04
Permanent pastures (% cover)	-0.1	-0.34	**-0.93**	0.03	-0.03	-0.09
Annual dry crops and fallows (% cover)	-0.19	-0.32	**0.91**	0.07	-0.07	0.03
Mean patch area of crops (ha)	**-0.62**	**-0.61**	0.15	-0.05	0.11	-0.22
Eigenvalue	*4.00*	*2.79*	*1.78*	*1.46*	*1.14*	*1.26*
Percentage of variance (%)	*26.7*	*18.1*	*11.8*	*9.7*	*7.6*	*8.4*

[1] Agricultural to natural habitats.

[2] Agricultural habitats to open woodlands.

[3] Permanent pastures to annual dry crops and fallows.

[4] Arable land with scattered trees.

[5] Water bodies.

[6] Annual irrigated crops.

Table S4.5 - Summary of models relating β-diversity metrics (total beta diversity, β_{Tot}; species replacement, β_{Repl}; species richness difference, $\beta_{RichDiff}$) to variation in landscape heterogeneity in **high-intensity farmland**. Models were built separately for two time periods using multiple regression on distance matrices (MRM). Landscape heterogeneity was defined as the pairwise Euclidean distances between the scores of transects along the axes of a principal component analysis (PCA) of habitat variables, with varimax rotation ($\Delta PC\#_{high}$). The matrix of geographical distances (Dist) between sampling point was included to account for spatial autocorrelation. Statistical significance of model coefficients was estimated using a permutation procedure: § $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Model coefficients with $P < 0.10$ are given in bold and shaded. The interpretation of each axis used to describe landscape heterogeneity is in Table S4.3.

Beta diversity metric	Intersect	Dist	$\Delta PC1_{high}$	**$\Delta PC2_{high}$**	**$\Delta PC3_{high}$**	$\Delta PC4_{high}$	**$\Delta PC5_{high}$**	R^2	*F*	*P*
1995-1997										
All species										
β_{Tot}	0.61	0.004	0.01	-0.02	0.02	-0.01	-0.01	0.05	3.40	0.593
β_{Repl}	0.27	0.004	0.03	0.00	0.03	0.00	**-0.05***	0.07	4.83	0.168
$\beta_{RichDiff}$	0.34	0.000	-0.02	-0.03	-0.01	-0.02	**0.03***	0.04	2.27	0.353
Farmland										
β_{Tot}	0.60	0.004	0.00	-0.02	0.01	-0.01	-0.01	0.03	1.76	0.895
β_{Repl}	0.27	0.003	0.02	0.02	0.02	-0.01	-0.04	0.05	3.43	0.417
$\beta_{RichDiff}$	0.33	0.001	-0.03	-0.04	-0.01	-0.01	0.03	0.04	2.65	0.380
Steppe										
β_{Tot}	0.48	0.000	0.00	-0.02	-0.02	-0.03	-0.01	0.04	2.09	0.828
β_{Repl}	0.24	0.000	0.01	-0.02	**-0.05§**	-0.01	-0.02	0.04	2.61	0.612
$\beta_{RichDiff}$	0.23	0.000	-0.01	0.00	0.03	-0.02	0.02	0.05	2.77	0.540
SPEC1-3										
β_{Tot}	0.67	0.006	-0.01	-0.03	-0.04	-0.04	-0.03	0.04	2.85	0.747
β_{Repl}	0.28	-0.001	-0.01	0.01	-0.01	-0.01	-0.04	0.02	0.96	0.960
$\beta_{RichDiff}$	0.38	0.006	-0.01	-0.04	-0.02	-0.03	0.01	0.03	1.68	0.837
2010-2012										
All species										
β_{Tot}	0.19	-0.002	-0.02	0.00	0.03	0.00	-0.01	0.05	3.29	0.623
β_{Repl}	0.44	0.002	0.03	**0.03***	-0.01	0.01	0.01	0.08	5.72	0.213
$\beta_{RichDiff}$	0.19	-0.002	-0.02	0.00	0.03	0.00	-0.01	0.05	3.29	0.632
Farmland										
β_{Tot}	0.18	-0.001	0.00	0.02	0.01	0.01	0.00	0.02	1.42	0.919
β_{Repl}	0.44	0.000	0.01	**0.02***	0.00	0.00	0.00	0.03	1.82	0.729

Beta diversity metric	Intersect	Dist	ΔPC1$_{high}$	**ΔPC2$_{high}$**	**ΔPC3$_{high}$**	ΔPC4 $_{high}$	**ΔPC5$_{high}$**	R^2	*F*	*P*
$\beta_{RichDiff}$	0.18	-0.001	0.00	0.02	0.01	0.01	0.00	0.02	1.42	0.914
Steppe										
β_{Tot}	0.29	0.000	0.03	0.00	-0.01	0.03	-0.04	0.07	4.62	0.536
β_{Repl}	0.22	0.000	-0.03	**0.04**[§]	0.02	-0.02	0.01	0.05	3.13	0.562
$\beta_{RichDiff}$	0.29	0.000	0.03	0.00	-0.01	0.03	-0.04	0.07	4.62	0.537
SPEC1-3										
β_{Tot}	0.17	0.002	0.02	0.01	0.01	0.01	0.00	0.03	2.05	0.735
β_{Repl}	0.45	-0.002	-0.01	0.02	0.01	0.00	0.00	0.01	0.94	0.907
$\beta_{RichDiff}$	0.17	0.002	0.02	0.01	0.01	0.01	0.00	0.03	2.05	0.737

Table S4.6 - Summary of models relating β-diversity metric (total beta diversity, β_{Tot}; species replacement, β_{Repl}; species richness differences, $\beta_{RichDiff}$) to variation in landscape heterogeneity in **low-intensity farmland**. Models were built separately for two time periods using multiple regression on distance matrices (MRM). Landscape heterogeneity was defined as the pairwise Euclidean distances between the scores of transects along the axes of a principal component analysis (PCA) of habitat variables, with varimax rotation ($\Delta PC\#_{low}$). The matrix of geographical distances (Dist) between sampling point was included to account for spatial autocorrelation. Statistical significance of model coefficients was estimated using a permutation procedure: § $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Model coefficients with $P < 0.10$ are given in bold and shaded. The interpretation of each axis used to describe landscape heterogeneity is in Table S4.4.

Beta diversity metric	Intersect	**Dist**	**$\Delta PC1_{low}$**	**$\Delta PC2_{low}$**	$\Delta PC3_{low}$	**$\Delta PC4_{low}$**	$\Delta PC5_{low}$	$\Delta PC6_{low}$	R^2	*F*	*P*
1995-1997											
All species											
β_{Tot}	0.64	**0.004****	**0.02***	**0.04****	0.00	-0.01	-0.01	0.00	0.15	**22.06**	**<0.001**
β_{Repl}	0.40	**0.003§**	**0.03***	0.02	-0.01	-0.01	0.00	0.00	0.04	5.82	0.208
$\beta_{RichDiff}$	0.23	0.001	-0.01	0.02	0.02	0.00	-0.01	0.00	0.02	2.46	0.676
Farmland											
β_{Tot}	0.64	**0.004****	**0.02***	**0.03****	0.00	-0.01	-0.01	0.00	0.11	**15.83**	**0.001**
β_{Repl}	0.36	**0.003§**	**0.04***	**0.05****	0.00	-0.01	0.01	0.00	0.10	**13.60**	**0.034**
$\beta_{RichDiff}$	0.27	0.000	**-0.02§**	-0.02	0.01	0.00	-0.02	0.00	0.04	4.78	0.466
Steppe											
β_{Tot}	0.50	**0.005****	**0.03****	**0.03***	0.00	-0.01	0.00	-0.01	0.09	**12.90**	**0.004**
β_{Repl}	0.24	**0.006****	0.03	0.01	0.01	-0.01	-0.01	0.00	0.04	5.41	0.233
$\beta_{RichDiff}$	0.26	-0.001	0.01	0.02	-0.01	0.01	0.01	0.00	0.02	2.56	0.743
SPEC1-3											
β_{Tot}	0.58	**0.005*****	**0.02***	**0.03****	0.01	-0.01	-0.01	0.00	0.12	**17.09**	**<0.001**
β_{Repl}	0.29	0.003	**0.07****	**0.05***	-0.01	-0.01	0.00	0.00	0.11	**16.04**	**0.013**
$\beta_{RichDiff}$	0.29	0.002	**-0.05***	-0.01	0.02	0.00	-0.02	0.00	0.06	7.86	0.327
2010-2012											
All species											
β_{Tot}	0.630	**0.004*****	**0.02§**	**0.03****	0.00	0.01	0.00	0.00	0.16	**24.65**	**<0.001**
β_{Repl}	0.422	0.000	-0.01	**0.04***	-0.01	0.01	0.01	0.00	0.08	**11.09**	**0.098**
$\beta_{RichDiff}$	0.208	**0.004***	0.02	-0.01	0.01	0.00	-0.01	0.00	0.05	6.19	0.411
Farmland											
β_{Tot}	0.624	**0.005*****	0.01	**0.02***	0.00	0.01	0.00	-0.01	0.11	**15.76**	**0.002**

Beta diversity metric	Intersect	**Dist**	**ΔPC1$_{low}$**	**ΔPC2$_{low}$**	ΔPC3$_{low}$	**ΔPC4$_{low}$**	ΔPC5$_{low}$	ΔPC6$_{low}$	R^2	*F*	*P*
β_{Repl}	0.397	0.000	0.01	**0.04***	-0.01	0.01	0.02	-0.02	0.08	10.53	0.102
$\beta_{RichDiff}$	0.227	**0.005***	0.00	-0.02	0.01	0.00	-0.02	0.01	0.05	6.51	0.404
Steppe											
β_{Tot}	0.470	**0.005****	0.01	**0.03***	0.00	0.00	0.01	-0.01	0.08	**11.75**	**0.009**
β_{Repl}	0.294	0.002	0.02	-0.01	-0.01	**-0.03***	0.01	-0.01	0.05	**6.15**	**0.099**
$\beta_{RichDiff}$	0.176	**0.003***	-0.01	**0.04***	0.01	**0.04***	0.00	-0.01	0.10	**14.12**	**0.011**
SPEC1-3											
β_{Tot}	0.586	**0.005****	0.01	**0.03****	-0.01	0.01	-0.01	-0.01	0.14	**20.18**	**0.001**
β_{Repl}	0.335	0.002	**0.03***	**0.04***	-0.01	**0.03§**	0.00	-0.01	0.09	**12.19**	**0.008**
$\beta_{RichDiff}$	0.250	**0.003***	**-0.02§**	0.00	0.00	-0.02	-0.01	0.01	0.04	4.93	0.315

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Chapter 5

General discussion

"We abuse land because we regard it as a commodity belonging to us. When we see land as a community to which we belong, we may begin to use it with love and respect."

"We shall never achieve harmony with land, any more than we shall achieve absolute justice or liberty for people. In these higher aspirations the important thing is not to achieve, but to strive."

A Sand County Almanac, and Sketches Here and There,
Aldo Leopold (1949)

5. General discussion

Conserving biodiversity on farmland is an essential element of worldwide efforts for reversing the global biodiversity decline (Krebs *et al.* 1999; Donald *et al.* 2006; Sutcliffe *et al.* 2015). However, managing farmland landscapes is complex, because biological diversity within these landscapes is constrained by a number of interacting and changing socioecological factors such as biophysical conditions, agricultural policies and socio-economic drivers, which may affect the effectiveness of conservation actions (Donald *et al.* 2001; Hinsley & Gillings 2012).

This thesis provides three case studies which are outlined and thoroughly discussed in **Chapters 2 to 4** (Santana *et al.* 2014, 2017a,b, respectively), where breeding bird communities living in open Mediterranean farmland landscapes of southern Portugal were used as model system to understand how biological diversity may vary in space and time in relation to conservation actions, agricultural policies, and landscape dynamics. These case studies provided insights to the design and evaluation of conservation actions required to enhance conservation outcomes within agricultural landscapes in the Mediterranean region. Specifically, this model system was used to provide answers to three main questions with broad implications for biodiversity conservation in Europe and elsewhere: What is the effectiveness of conservation funding on farmland?; What landscape components need to be considered when managing farmland for conservation?; How can beta diversity inform conservation actions on farmland?

This chapter presents the key results from these studies, some general guidelines to design and evaluate conservation actions on farmland (Fig. 5.1), with a particular focus on the birds of open Mediterranean farmland (Fig. 5.2), and some future research prospects.

5.1 Key results

5.1.1 What is the effectiveness of conservation funding on farmland?

Evaluating the effectiveness of conservation funding is crucial for correct allocation of limited resources devoted to biodiversity conservation. The case study presented in **Chapter 2** (Santana *et al.* 2014) evaluated the effects of long-term conservation investment in Natura 2000 farmland, by analyzing temporal variation in bird species richness and abundance, considering the overall bird assemblage, the assemblage of birds of conservation concern, and the assemblages of birds with similar habitat affinities. The study focused on two contrasting farmland areas: i) the Natura 2000 special

protection area (SPA) of Castro Verde, which benefited during two decades from protection regulations, LIFE conservation projects, and agri-environment schemes; and ii) a control farmland area under agriculture intensification and without conservation-oriented investments. This study showed mixed effects of long-term conservation investment in Natura 2000 farmland, suggesting that enhancing the effectiveness of conservation investment in Natura 2000 farmland may require a greater focus on the wider biodiversity in addition to that currently devoted to flagship species, as well as improved matching between conservation and agricultural policies.

Conservation investment in the SPA had positive effects on flagship species (great bustard *Otis tarda*, little bustard *Tetrax tetrax*, and lesser kestrel *Falco naumanni*), and on species associated with fallows (calandra lark *Melanocorypha calandra* and little bustard), which were the main targets of conservation investment. However, temporal trends in the control area appeared most favorable for the total bird assemblage, as well as for the farmland, ground-nesting and steppe groups of species (i.e. ploughed and cereal fields associated species), and even for the Species of European Conservation Concern (SPEC1-3). Positive trends within the SPA for populations of highly threatened flagship species supports the view that targeted efforts combining legal regulations and adequate funding schemes may deliver major conservation benefits (Batáry *et al*. 2011, Bretagnolle *et al.* 2011, Baker *et al.* 2012). The observed trends were probably a consequence of targeted LIFE projects, which funded the purchase and management of critical areas, and the improvement of breeding and foraging habitats (Pinto *et al.* 2005, Catry *et al.* 2009, Moreira *et al.* 2012). Simultaneously, as it is further explored in **Chapters 3** and **4** (Santana *et al.* 2017a,b, respectively)**,** there were likely benefits from legal regulations preventing afforestation, the conversion to permanent crops, and the expansion of irrigated agriculture, which have caused detrimental changes in landscape composition and structure outside the SPA. The direct effect of AES is uncertain, because they apparently failed to promote the traditional rotational farming system (Ribeiro *et al.* 2014), though they may have helped prevent land abandonment (Stoate *et al.* 2009).

The observed less favorable trends in the SPA for the other steppe birds suggests that investment concentrating on charismatic species does not necessarily lead to the conservation of the overall steppe bird assemblage due to land use changes (Caro 2010). This is because the CAP reform of 2003 provided economic incentives promoting a shift to specialized livestock production and thus declines in the traditional farming system (Ribeiro *et al.* 2014), which were not offset by the agri-environment schemes supporting biodiversity-friendly agricultural practices in the SPA. There was thus a progressive increase in cover by pastures at the expenses of cereal and ploughed fields,

which was far more marked in the SPA than in the control. The expansion of pastures should have benefited species typically associated with fallows, because the two habitats may be structurally similar (Suárez *et al.* 1997; Delgado & Moreira 2000). No effects were found for species associated with cereal fields, because declines in this habitat were similar in the SPA and the control. In contrast, species associated with ploughed fields declined in the SPA due to reductions in cereal cultivation, but they increased in the control because recently planted olive groves have bare ground akin to ploughed fields. These results suggest that a mosaic of arable crops and pastures may be critical to maintain conditions for steppe birds with contrasting habitat requirements, further supporting the importance of landscape scale factors to promote conservation on farmland (Concepción & Diaz 2010; Concepción *et al.* 2012). Conservation investment appeared unable to preserve such mosaics, probably because livestock specialization driven by CAP was not counterbalanced by adequate regulations or funding schemes.

5.1.2 What landscape components need to be considered when managing farmlands for conservation?

Common approaches to conserving biodiversity on farmland may involve: i) improving the natural component of the landscape by increasing the amount of natural and semi-natural habitats; ii) improving the production component of the landscape by increasing the amount of biodiversity-friendly crops; or alternatively, iii) enhancing the landscape heterogeneity, without necessarily changing composition. The case study presented in **Chapter 3** (Santana *et al.* 2017a) examines whether managing landscape composition or heterogeneity, or both, would be required to achieve conservation benefits on avian diversity, by analysing spatial and temporal variation in bird species richness with variables describing the composition, and the compositional and configurational heterogeneity, of the natural and production components of the landscape. This study showed that the composition of the natural and the production components had far stronger effects than those of their compositional or configurational heterogeneity (*sensu* Fahrig *et al.* 2011), suggesting that the composition of the production component of the landscape needs to be carefully considered when managing farmland for biodiversity, particularly in open Mediterranean farmland landscapes where there is a range of species tightly associated with crops and pastures for breeding and foraging (Reino *et al.* 2009, 2010; Concepción & Díaz 2011; Moreira *et al.* 2012).

This case study supports the expectation that the natural component of the landscape should have a strong effect on total species richness, in particular that of woodland and shrubland birds, while the effects of the production component should also be strong, particularly on farmland and steppe bird species. The effects of the production

component are generally stronger on farmland and steppe birds, probably because they often live within the production area, and so they should be particularly affected by the identity and amount of different crop types represented in farmland landscapes (Chamberlain *et al.* 2001; Wilson *et al.* 2005; Stoate *et al.* 2009; Butler *et al.* 2010; Rey 2011; Berg *et al.* 2015; Hiron 2015; Josefsson *et al.* 2017). However, in some circumstances, the production component may also affect non-farmland birds, such as woodland and shrubland birds. This may be the case of the orchards (e.g. olive groves), which have structural similarities with woodlands, and may thus attract species that otherwise would be rare or absent in open arable farmland (Rey 2011). As a consequence, cover by these permanent crops may increase total species richness, although these habitats are known to be avoided by a range of steppe birds associated with open farmland habitats (Stoate *et al.* 2009). However, the influence of the production component may change over time, as its influence on bird assemblages species richness may be related to the prevalence of the different crop types across the landscape.

In marked contrast to other studies proposing heterogeneity as the key driver of farmland biodiversity (Benton *et al.* 2003; Fahrig *et al.* 2011), this study showed that the effects of heterogeneity were relatively weak and inconsistent, with few clear relationships between species richness and variables describing the diversity of land cover types (i.e., compositional heterogeneity) or the spatial arrangement of such cover types (i.e., configurational heterogeneity). The contrast between results from this case study and the importance normally given to heterogeneity on farmland may be a consequence of some particularities of the study, including the use of coarse land cover categories, the limited range of variation in landscape heterogeneity, and the particular ecology of bird communities living on the open Mediterranean farmland. However, it also indicates that the importance of heterogeneity across farmland landscapes probably depends on local ecological characteristics and agricultural land uses. Therefore, efforts to promote the conservation of biodiversity based on managing landscape heterogeneity, without necessarily changing composition, may not be adequate in every case, because farmland diversity in at least some landscapes may be far more affected by the identity of crops produced, rather than by their diversity or spatial configuration.

5.1.3 How can beta diversity inform conservation actions on farmland?

Spatial variation in species composition (β-diversity) is an important component of farmland biodiversity, which together with local richness (α-diversity) drives the number of species in a region (γ-diversity). However, β-diversity is seldom used to inform conservation. The case study presented in **Chapter 4** [Santana *et al.* 2017a] evaluates the value of β-diversity to guide conservation on farmland by first quantifying the

contribution of bird α- and β-diversity to variation in γ-diversity in low- and high-intensity Mediterranean farmland, before (1995-1997) and after (2010-2012) the CAP reform of 2003, then relating changes in β-diversity to landscape heterogeneity. This study stresses the value of β-diversity to understand impacts of agricultural policies and conservation actions, but also highlights the need to evaluate β-diversity changes against specific conservation goals.

Specifically, in low-intensity farmland, spatial variation in species composition (β-diversity) was largely stable over time, reflecting a positive conservation outcome related to persistence of landscape heterogeneity patterns required by endangered steppe bird species. In contrast, β-diversity in high-intensity farmland was favoured by increases in landscape heterogeneity driven by olive grove expansion, contributing to enhancement of total bird diversity. This study shows that β-diversity is important for understanding the consequences of land-use changes, as focusing solely on α-diversity would have missed important links between biodiversity and anthropogenic drivers, thus supporting previous suggestions that β-diversity may be essential to capture processes that are hard or impossible to detect using only local diversity metrics (Clough *et al.* 2007; Gaston *et al.* 2007; Monnet *et al.* 2014; Socolar *et al.* 2016; Żmihorski *et al.* 2016). Also, the analysis of β-diversity helps to identify the main land-use types shaping functional landscape heterogeneity (*sensu* Fahrig *et al.* 2011), which is critical for farmland conservation management. This is because, although there may exist a variety of land uses shaping a range of habitat gradients, only heterogeneity associated with some gradients could be considered functional, in the sense that they strongly affect spatial variation in assemblage composition. Finally, temporal variations in β-diversity may be used to assess biodiversity trends, which should be interpreted in the context of local conservation objectives, as higher β-diversity *per se* does not necessarily equate to higher conservation value (Socolar *et al.* 2016). Therefore, management of landscape heterogeneity and β-diversity should be fine-tuned in relation to well-defined conservation goals (e.g. Báldi & Batáry 2011).

5.2 Conservation implications

5.2.1 How to design conservation actions on farmland?

This thesis provides some insights on the design of conservation actions that are critical to enhance conservation outcomes on farmland (Fig. 5.1). Specifically, conservation actions should focus on wider biodiversity alongside of flagship species; focusing investment on flagship species may help the recovery of highly threatened species, but without wider benefits to less charismatic species of conservation concern (**Chapter 2**

[Santana *et al.* 2014]). Also, managing farmland landscapes for conservation needs to consider both composition and heterogeneity of the landscape. However, in areas where a range of species of conservation concern is strongly associated with crop habitats, conservation actions should focus primarily on the composition of the production component, by striving to maximise the prevalence of biodiversity-friendly crops (**Chapter 3** [Santana *et al.* 2017a]). Finally, conservation effectiveness within farmlands requires a match between conservation actions and agricultural policies to avoid that they may be offset by more attractive economic incentives (**Chapter 2** [Santana *et al.* 2014]). This is because agri-environmental funding schemes designed for the farm level can be surpassed by more general agricultural policies and small scale structural and biophysical factors constraining farmer options (Ribeiro *et al.* 2014). The farming system approach may provide a practical solution to this by grouping farms according to their agricultural typology and by providing information on the key factors driving major land-use transitions (Ribeiro *et al.* 2014). Specifically, following this approach conservation actions would be designed to meet the specificities and constraints of each farming system, thereby optimizing investments on the farming systems that need to be maintained and encouraging transitions benefiting biodiversity in unfavourable farming systems (Ribeiro *et al.* 2014).

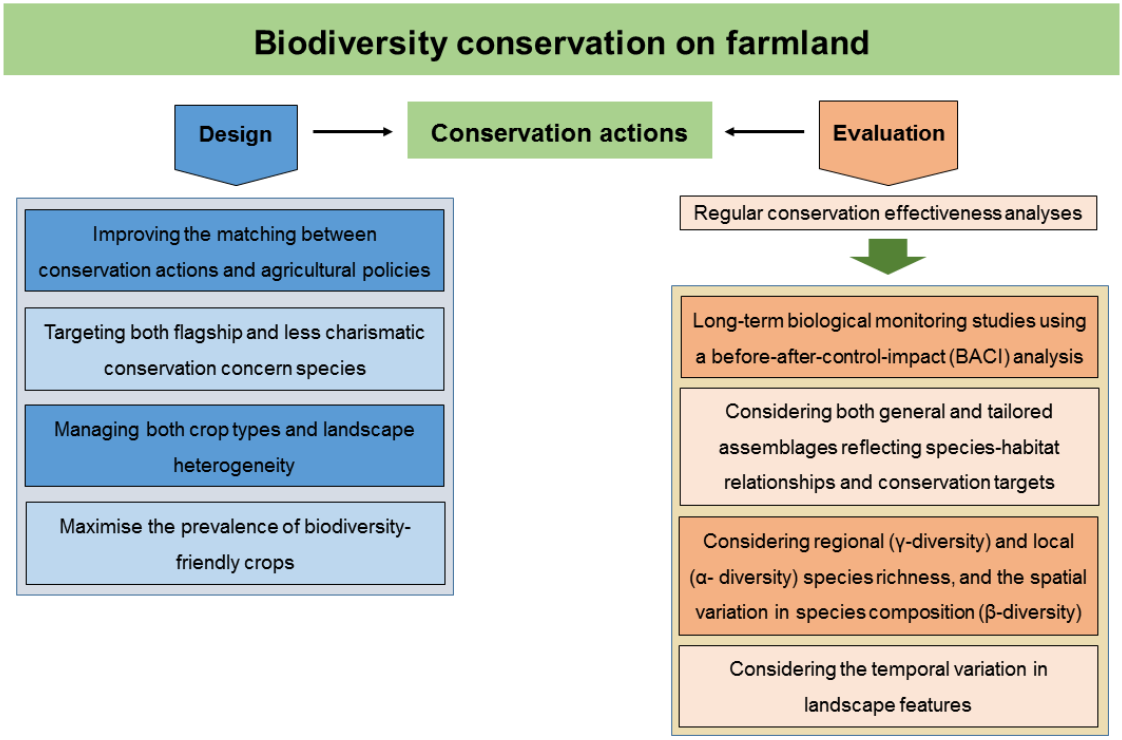

Fig. 5.1 - Framework for the design and evaluation of conservation actions on farmland, highlighting the key ideas that need to be considered when designing conservation management actions, as well as the guidelines that need to be followed when evaluating the efficacy of such actions.

5.2.2 How to evaluate conservation actions on farmland?

This thesis provides a roadmap for evaluating conservation effectiveness to inform conservation actions and enhance conservation outcomes in farmland landscapes (Fig. 5.1). Analysis of conservation's effectiveness must must be regularly performed to account for important changes in agricultural policies (e.g. the reforms of the CAP in the case of the Natura 2000 protected areas) (**Chapter 2** [Santana *et al*. 2014]) and should consider the following guidelines. First, monitoring programs need to be established at the beginning of the implementation of conservation measures, to be used as a baseline against which future changes can be addressed. These programs must comprise species sampling and habitat characterization, within both the area of intervention and in a nearby control area where conservations measures have not been implemented (**Chapter 2** [Santana *et al*. 2014]). Second, conservation effectiveness analysis should focus on both impact and control areas using a before-after-control-impact (BACI) design, where the interest should be on the interaction between the area (in and outside the conservation area) and the period (before and after the implementation of conservation actions and/or changes in agricultural policies) (**Chapter 2** [Santana *et al*. 2014]). This analysis provides information on what trends in the protected farmland are above or below those expected from trends observed in the control area. Third, diversity parameters should be specifically tailored to reflect the outcome of conservation interventions, focusing not only on the total community but also on groups of species of conservation concern that are specialized in the habitat types which that are the focus of conservation actions (**Chapter 2** [Santana *et al*. 2014]). Fourth, diversity metrics to be analyzed should include local metrics such as species richness (α-diversity) and abundance, but also the spatial variation in species diversity and composition across the landscape (β-diversity) (**Chapters 2 and 4** [Santana *et al*. 2014, 2017b]). The analysis of β-diversity is important because it allows identification of the main land-use types shaping functional landscape heterogeneity (*sensu* Fahrig *et al.* 2011), which is critical for farmland conservation management (**Chapter 4** [Santana *et al*. 2017b]). Finally, landscape scale habitat patterns must be monitored along with diversity patterns as they constrain conservation outputs and are shaped by both conservation actions and agricultural policies (**Chapters 3 and 4** [Santana *et al*. 2017a,b]). Overall, different diversity metrics (α-, β- and γ-diversity) for specific groups of species must be linked to habitat patterns reflecting changes in agricultural policies, and conservation goals must be considered to evaluate conservation effectiveness within farmland (**Chapter 2 to 4** [Santana *et al*. 2014; 2017a,b]).

5.2.3 How to manage open Mediterranean farmland for biodiversity conservation?

Through the nature of its case studies, this thesis also provides specific insights on conserving bird diversity on open Mediterranean farmland, both in low- and high-intensity farmland areas (Figure 5.2). Specifically, in low-intensity farmland areas, where a large number of birds of high conservation concern are associated with open habitats, management should be directed to increase steppe bird species richness and abundance both at local [α-diversity], and regional [γ-diversity] scales, but not necessarily that of the overall avian community (**Chapter 2** [Santana *et al.* 2014]). Also, conservation management within these areas should be directed to maintain a stable β-diversity, with any temporal increases in β-diversity potentially reflecting negative conservation outcomes, as they may be associated with the spatial replacement of steppe bird species by species of low conservation concern (**Chapter 4** [Santana *et al.* 2017b]). Specifically, landscapes should be managed to maintain the dominance of open agricultural habitats (i.e, large areas occupied by rain-fed cereals, fallows, and extensive pastureland), even though this may reduce landscape heterogeneity, and overall β- and γ-diversity (**Chapter 2 to 4** [Santana *et al.* 2014, 2017a,b]).

Evaluation of the conservation effectiveness within low-intensity farmland areas thus needs to be focused on groups of species reflecting the species-habitat relationships with the elements of the traditional agricultural mosaic (e.g. rain-fed cereal, fallow, and ploughed fields). This is because trends in more general groups (e.g. total, farmland, and even SPEC1-3 assemblages) may increase due to shrub encroachment, afforestation, and expansion of permanent crops (Diaz *et al.* 1998; Reino *et al.* 2009, 2010, Santana *et al.* 2012), but these processes are detrimental for the relatively species-poor but highly specialized assemblage of steppe birds that include several species of high conservation concern (Suárez *et al.* 1997; Delgado & Moreira 2000; Concepción & Díaz 2010; Reino *et al.* 2010).

In contrast, conservation actions in high-intensity farmland should be directed to increase α, β- and γ-diversity rather than the diversity of any particular species group (e.g. Fahrig *et al.* 2011; Karp *et al. 2*012) (**Chapter 2 to 4** [Santana *et al.* 2014, 2017a,b]). Specifically, the preservation of a patchwork of arable and permanent crops may be a key management goal, as this may increase landscape functional heterogeneity, thus providing conditions for farmland, shrubland and woodland species at the landscape scale (**Chapter 3** [Santana *et al*. 2017a]). However, continued monitoring of β-diversity in these areas is needed to account for potential negative outcomes from a possible landscape homogenization due to expansion of permanent crops, which would reflect in decreases of total diversity **Chapter 4** [Santana *et al*. 2017b]).

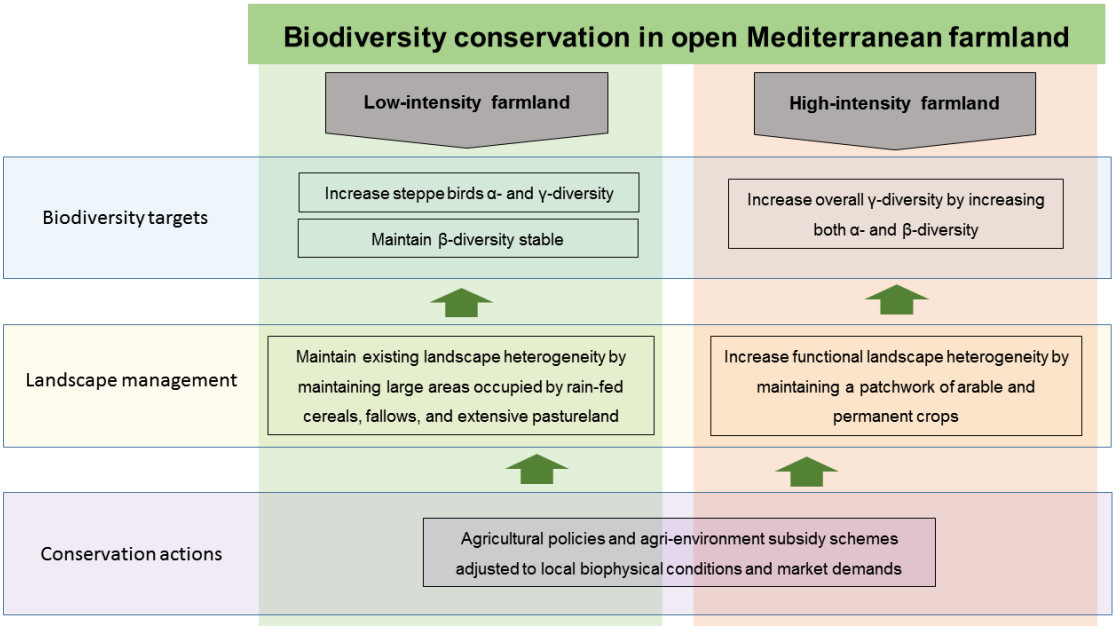

Fig. 5.2 - Framework for the management of open Mediterranean farmland, underlining the contrast of biodiversity targets and landscape management prescriptions in low-intensity and high-intensity farmland.

Conservation actions in both low- and high-intensity farmland areas would require agricultural policies and agri-environmental funding schemes adjusted to local biophysical conditions and market demands, to avoid conservation measures to be offset by more attractive economic incentives from general agricultural policies (Ribeiro *et al.* 2014; Santana *et al.* 2014; Ribeiro *et al.* 2016a,b). Solutions to maintain landscape heterogeneity on high-intensity farmland areas would however require additional socioeconomic studies for the possible regulation mechanisms to avoid undue expansion of permanent crops, but this is out of the scope of this thesis.

5.3 Implications for future research

The Natura 2000 is the main network of protected areas in Europe and is the centerpiece of European Union nature and biodiversity policy (EC 2013). Most of Natura 2000 land is privately owned, and an important part of it is devoted to agriculture. Therefore, establishing and managing these areas involves considerable conservation investment (EC 2013), and evaluating their effectiveness is thus considered a high priority to ensure appropriate allocation of resources (Kleijn *et al.* 2011; Hochkirch *et al.* 2013). The case study presented in **Chapter 2** (Santana *et al.* 2014) indicates that conservation investment in the special protection area of Castro Verde had positive effects on populations of highly threatened flagship species, but less positive results were found for some groups of species that were also targets of conservation investment. Positive trends appeared to be linked to legal regulations preventing conversion to land uses

detrimental to these species, to targeted LIFE programs that allowed the purchase and management of critical areas, and to the improvement of breeding and foraging habitats (Pinto *et al.* 2005; Catry *et al*. 2009; Moreira *et al.* 2012). Moreover, AES may have helped prevent land abandonment (Stoate *et al.* 2009). However, the less positive results appeared related to the conflict between agricultural and environmental policies. Conservation investment appeared unable to preserve the traditional rotational farming system (Ribeiro *et al.* 2014), which is critical to maintain conditions for steppe birds with contrasting habitat requirements (Concepción & Diaz 2010; Concepción *et al.* 2012), probably because livestock specialization driven by the CAP reform of 2003 was not counterbalanced by adequate conservation funding schemes. Future research should be focused on long-term evaluations of conservation investment, to understand how agricultural and conservation policies interact with biodiversity on this and other farmland systems, and also accounting for the effects of the ongoing reform of the CAP 2014-2020.

There are increasing efforts to promote the conservation of biodiversity on farmland while minimising impacts on economic output, and enhancing landscape heterogeneity has been recommended as a key solution to achieve this goal (Fahrig *et al.* 2011). The case study presented in **Chapter 3** (Santana *et al.* 2017a) suggests that this option may not be adequate in every case, because farmland biodiversity in some landscapes may be far more affected by the identity of crops produced, rather than by their diversity or spatial configuration. Future research is thus needed to explore under what circumstances major benefits can be achieved by changing landscape heterogeneity (*sensu* Fahrig *et al.* 2011), and where such benefits require focusing primarily on what crops are grown and how they are managed.

Spatial variation in species composition (β-diversity) is an important component of farmland biodiversity seldom used to inform conservation, due to limited understanding of its responses to agricultural management, and lack of clear links between β-diversity changes and conservation outcomes. The case study presented in **Chapter 4** (Santana *et al*. 2017b) shows that β-diversity can be used to provide practical insights on the management of specific farmland areas beyond those supported solely on information from the local patterns of assemblage richness and composition (i.e. α-diversity) (e.g. Delgado & Moreira 2000; Stoate *et al*. 2003; **Chapters 2 and 3** [Santana *et al.* 2014, 2017a]). This is because β-diversity increased with increasing landscape heterogeneity, which in the high-intensity farmland was associated with the expansion of olive groves, suggesting that a patchwork of arable and permanent crops may be a key management goal in that area, as this provides conditions for both farmland and woodland and shrubland species at the landscape scale (**Chapter 3** [Santana *et al*.

2017a]), and thus high β- and γ-diversity. However, further expansion of olive groves may turn out to be negative if it leads to progressive homogenization of the landscape, requiring this potential outcome to be assessed through continued monitoring of β-diversity. Further research is needed in order to understand how β-diversity would vary under different landscape feature scenarios including a range of spatial arrangements, and sizes of olive groves patches, and how these affect regional diversity trends.

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